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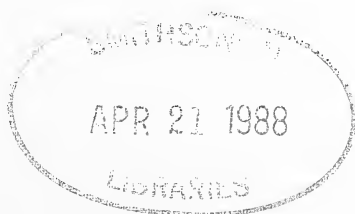
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**Cover illustration:** Computer-drawn figure of Dakota skipper, *Hesperia dacotae* (Skin.), nectaring on narrow-leaved purple coneflower, *Echinacea angustifolia* DC. Drawing originally executed freehand in the Macintosh application Fullpaint and embellished with FatBits, exported to SuperPaint and further embellished with LaserBits, then produced on a LaserWriter. Cover version is 50% width of LaserWriter version. Submitted by Ronald A. Royer, Division of Science, Minot State University, Minot, North Dakota 58701.



# JOURNAL OF THE LEPIDOPTERISTS' SOCIETY

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## SPEYERIA ATLANTIS IN COLORADO: REARING STUDIES CONCERNING THE RELATION BETWEEN SILVERED AND UNSILVERED FORMS

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**ABSTRACT.** *Speyeria atlantis* in the SE Rocky Mts. occurs in two forms, silvered and unsilvered, that could be mere forms or separate species. Nine wild females laid eggs and produced adults in the laboratory. Offspring resembled mothers in most cases, except for two mothers about half silvered and one mother about one-third silvered that produced nearly unsilvered offspring. The two forms have the same courtship, without obvious courtship barriers between them, and male pheromones smell the same. Silvered and unsilvered adults have differently colored larvae. The two forms can differ in habitat, and adults actively select different habitats. The two are probably forms of the same species.

**Additional key words:** Nymphalidae, habitat selection, polymorphism, courtship.

The relation between silvered and unsilvered forms of *Speyeria atlantis* (Edw.) has puzzled many people (Scott 1986b). Thus Grey et al. (1963) discussed the two forms in the Black Hills of South Dakota, where the silvered form with chocolate ventral hindwing (*a. atlantis*) predominates in wet meadow areas, and the unsilvered form with reddish-brown ventral hindwing (*a. hesperis* Edw. = *a. lurana* dosP. & G.) prevails in drier areas. From a locality with 44% silvered adults, W. Evans (in Grey et al. 1963:146) reared 3 silvered offspring with chocolate ventral hindwing from silvered mothers with chocolate ventral hindwing, and 26 unsilvered plus at least 1 silvered offspring with a reddish-brown ventral hindwing from unsilvered mothers with a reddish-brown ventral hindwing. The exact number of mothers contributing was not known, but was probably one or two for each form. Evans noted that the double dorsal stripes were light brown on *atlantis* larvae, grayish white on *hesperis* larvae, and that *hesperis* pupae have more light-brown shading on the wing case than do *atlantis*. Grey et al. (1963) suggested that the two could be treated as separate species,

though they retained them in one species because they seem to intergrade in other western U.S. regions.

A similar situation occurs in SW Manitoba where a dark variety of silvered *a. atlantis* (*a. hollandi* F. & R. Cherm.) with chocolate ventral hindwing flies in mountains and forest, whereas a very pale silvered *a. dennisi* dosP. & G. usually with light-brown ventral hindwing flies on tallgrass prairie. They occur near each other. At Duck Mountain, adjacent populations show no intergradation (J. Troubridge pers. comm.). In this area, they behave as separate species, although westward they intergrade at Meadow Lake Park, Saskatchewan (Hooper 1973).

In Colorado E of the continental divide, the unsilvered form (*a. hesperis*) prevails in the mountain foothills, and as one goes higher in the mountains the silvered form (*a. atlantis*, = *a. electa* Edw.) gradually increases in frequency until it predominates in the Canadian Zone. Silvered forms in Colorado's Front Range usually have a chocolate-brown ventral hindwing, whereas unsilvered forms usually have a reddish-brown ventral hindwing, although this association sometimes breaks down; thus some silvered adults have a red-brown ventral hindwing, and some unsilvered ventral hindwing adults have a darker reddish-brown ventral hindwing. Females have a slightly darker ventral hindwing than males; a bilateral gynandromorph from Critchell, for instance, has a very red-brown ventral hindwing on the male side, a darker red-brown ventral hindwing on the female side.

The silvered or unsilvered color is due to light reflection from individual scales. Silver scales appear transparent through a microscope, but their surfaces reflect a white sheen (evidently due to structural interference of light) which causes the silver appearance. Unsilvered scales are cream in color because they appear to be filled with cream pigment, and their surfaces do not reflect light; their scale structure could be the same as silvered scales if the internal pigment blocks transmission of light through the scale to prevent light interference. So the difference between silvered and unsilvered scales could result solely from absence or presence of internal cream pigment. A given wing spot can be entirely cream (unsilvered), or it can be cream with a few silver scales, or the entire spot can be covered with silver scales. Potentially silvered spots occur in four series on the ventral hindwing: basal, postbasal, postmedian, and submarginal. In the basal series, the dot in the discal cell is more likely to have silver scales than the other spots. The postbasal series of spots is less likely to be silvered than the other series, and the basal and marginal series are most likely to be silvered in the mostly unsilvered forms.

To determine the relation between the forms in Colorado, I reared the eggs of selected females, especially those females of a form rare in



their population because these would have the greatest likelihood of mating with a male of the opposite form.

### REARING METHODS

To obtain eggs, females were collected from Colorado Front Range localities, brought to the laboratory, and placed in jars with *Viola nephrophylla* Green leaves and fed honey-water once per day. Most females lived about a week and laid several dozen eggs. Eggs hatch readily, but first-stage larvae diapause in nature, so to prevent diapause they were placed under constant light in tiny vials with a slice of green violet leaf. After a few days or weeks some larvae ended diapause and started to feed; these fed steadily until pupation on *V. nephrophylla* leaves. Three months were required to raise offspring of one female. Voucher specimens including larvae, pupal shells, and reared silvered and unsilvered adults are in the National Museum of Natural History, Washington, D.C.

### RESULTS

#### Silvering of Mothers and Offspring

A total of 104 adult offspring were reared from 9 mothers from 6 Colorado sites. Each site is described below.

Tinytown (2120 m), Jefferson Co., is a Transition Zone foothills valley bottom with ponderosa pine, douglasfir, willow, alder, honeysuckle, etc., along the creek; the hostplants *Viola canadensis* L. and *V. adunca* Smith (Scott 1986a) are common on the shaded gulch bottom and the base of the N-facing slope. Here 92% of adults had a reddish-brown ventral hindwing with mostly unsilvered spots, 6% were partly silvered (N = 6 half silvered, N = 1 mostly silvered), and 2% were fully silvered with a chocolate-brown ventral hindwing (N = 117). If the fully silvered mother mated at random, the father was probably unsilvered; yet all offspring were silvered (Table 1).

Corwina Park (2120 m), Jefferson Co., is a Transition Zone foothills wooded gulch draining N; the hostplants *V. adunca* and probably *V. canadensis* are in gulch-bottom shade and E-facing shaded slopes. Here 91% of adults were unsilvered with a red-brown ventral hindwing, 9% silvered with a chocolate-brown ventral hindwing (N = 21). If the completely silvered mother mated at random, the father was probably unsilvered; yet all offspring were fully silvered (Table 1).

O'Fallon Park (2100 m), Jefferson Co., is near Corwina Park, and is also a Transition Zone foothills wooded gulch draining N with the hostplants *V. adunca* and *V. canadensis* in gulch-bottom shade and E-facing shaded slopes. Here 83% were unsilvered with a red-brown ventral hindwing, 13% silvered with a chocolate-brown ventral hind-

TABLE 1. Extent of silvering on ventral hindwing spots, and color of basal two-thirds of ventral hindwing, of mothers and offspring. Numbers are proportions: for example, "1" under "base" means all scales on wing base spots are silvered, "1/5" under "postmedian" means 20% of scales of postmedian spots are silvered, "0" under "submarginal" means no scales of submarginal spots are silvered, etc., "gyn" is bilateral gynandromorph, "f" is female, and "m" is male.

Material	Sex	Ventral hindwing	Base	Postbasal	Postmed.	Submarg.
Tinytown, Jefferson Co., mother caught 20 July 1984						
Mother	1 f	chocolate	1	1	1	1
Offspring	27 m	chocolate	1	1	1	1
Offspring	19 f	chocolate	1	1	1	1
Corwina Park, Jefferson Co., mother caught 13 July 1985						
Mother	1 f	dark choc-brown	1	1	1	1
Offspring	2 m	dark red-brown	1	1	1	1
Offspring	2 f	choc-brown	1	1	1	1
Offspring	1f	dark choc-brown	1	1	1	1
O'Fallon Park, Jefferson Co., mother caught 12 August 1985						
Mother	1 f	red-brown	2/3	1/5	1/2	1/2
Offspring	1 m	very red-brown	0	0	1/4	1/3
Offspring	1 f	very red-brown	0	0	0	1/5
Offspring	1 f	very red-brown	2/3	0	0	1/2
Critchell, Jefferson Co., mother caught 3 August 1985						
Mother	1 f	red-brown	1/2	1/10	1/2	1/2
Offspring	8 f	very red-brown	0	0	0	0
Offspring	6 f	very red-brown	0	0	0	0
Offspring	1 gyn	very red-brown	0	0	0	0
Mt. Judge female B, Clear Creek Co., mother caught 8 August 1985						
Mother	1 f	red-brown	2/3	1/3	1/5	1/3
Offspring	1 m	very red-brown	0	0	0	1/6
Offspring	6 m	very red-brown	0	0	0	1/10
Offspring	1 m	very red-brown	0	0	0	1/5
Offspring	1 m	very red-brown	1/10	0	0	1/5
Offspring	1 m	very red-brown	1/5	0	0	1/10
Offspring	2 f	very red-brown	0	0	0	1/10
Offspring	1 f	very red-brown	0	0	0	0
Cherry Gulch, Jefferson Co., mother caught 17 July 1984						
Mother	1 f	red-brown	2/3	1/5	0	1/3
Offspring	1 f	very red-brown	1/4	0	0	1/3
Mt. Judge female D, Clear Creek Co., mother caught 8 August 1985						
Mother	1 f	dark red-brown	1/5	0	0	1/2
Offspring	2 m	very red-brown	0	0	0	0
Mt. Judge female F, Clear Creek Co., mother caught 8 August 1985						
Mother	1 f	red-brown	1/5	0	0	1/10
Offspring	1 m	very red-brown	0	0	0	1/10
Offspring	1 m	very red-brown	1/10	0	0	1/5
Mt. Judge female A, Clear Creek Co., mother caught 8 August 1985						
Mother	1 f	red-brown	0	0	0	1/5
Offspring	9 m	very red-brown	0	0	0	0
Offspring	3 f	dark red-brown	0	0	0	1/10
Offspring	1 f	dark red-brown	0	0	0	1/6
Offspring	1 f	red-brown	0	0	0	0
Offspring	1 f	red-brown	0	0	0	1/6
Offspring	2 f	very red-brown	0	0	0	0



wing, and 4% intermediate ( $N = 19$ ). If the nearly half-silvered mother mated at random, the father was probably unsilvered; all offspring were nearly unsilvered (Table 1).

Critchell (2370 m), Jefferson Co., is a shaded E-W streamside in the upper Transition Zone foothills, with ponderosa pine, douglasfir, various shrubs, grassy glades, and *V. canadensis* and *V. adunca*. Here 88% were unsilvered with a reddish brown ventral hindwing, 7% fully silvered, and 5% intermediate ( $N = 2$  half silvered,  $N = 1$  mostly silvered) ( $N = 53$ ). If the nearly half-silvered mother mated at random, the father probably was unsilvered; all offspring were completely unsilvered (Table 1).

Cherry Gulch (2100 m), Jefferson Co., is a Transition Zone foothills gulch at the base of a N-facing slope covered with douglasfir, *Holodiscus*, *Physocarpus*, other shrubs, and *Viola canadensis*. Here 97% were unsilvered with a reddish brown ventral hindwing, 3% silvered with a brown ventral hindwing ( $N = 69$ ). If the mostly unsilvered mother mated at random, the father was probably unsilvered; the single offspring was less silvered than the mother (Table 1).

Mt. Judge (2 km NE, 2770 m), Clear Creek Co., is a Canadian Zone valley bottom, with forest (spruce, pine, douglasfir, some aspen) beside grassy meadows, a tiny creek on the valley bottom, and *V. canadensis* and *V. nephrophylla*. Silvered adults with a chocolate ventral hindwing were most common, with a few silvered adults with a reddish brown ventral hindwing; but unsilvered adults with a red-brown ventral hindwing were also found, a few unsilvered adults with a brown ventral hindwing, and a few variably silvered intermediates. The upperside black lines vary from narrow to wide independent of ventral hindwing variation. Shape of silver spots varies between individuals, as does amount of black at the base of each silver spot, but this variation is also independent of degree of silvering. Four females from this site labeled A, B, D, and F, produced offspring (Table 1). If the Mt. Judge mothers mated at random, they probably mated with silvered males because 74% of males here were silvered (Table 2). However, because of habitat selection at this site (described in next section), and because all four mothers were found in mixed woods away from the creek where only 38% of males were silvered (Table 2), the mothers probably mated with unsilvered fathers. Mother B was about one-third silvered; her offspring were almost completely unsilvered. Mothers A, D, and F, and their offspring, were almost completely unsilvered.

### Habitat Selection and Movements

The Mt. Judge site displayed habitat selection by the forms (Table 2). In several meadows along the tiny creek 90% of adults were silvered,

TABLE 2. Frequency of color forms at Mt. Judge site, based on nine visits 1984 to 1987.

Silvering	Mixed woods away from creek		Meadows along creek	
	No. male	No. female	No. male	No. female
Mostly unsilvered	24	13	11	2
Half silvered	1	0	1	0
Completely silvered	15	8	72	53

10% unsilvered. In contrast, at the habitat edge near the head of the valley, away from the creek in mixed woods—tiny meadows edging the large meadow and in the adjacent meadow-edge, one-third (38%) of adults were silvered, and two-thirds (62%) unsilvered.

A small mark-recapture study was conducted at Mt. Judge in 1987 (31 July, 5, 9 Aug.), in which 33 adults were marked and 16 recaptured. Six unsilvered adults were marked (2 male, 4 female), and 3 females recaptured, all in the mixed woods, one after 5 days. Twenty-seven silvered adults were marked (14 male, 13 female), and 13 recaptured (7 male, 6 female), after up to 9 days, including 5 moves completely across the habitat, and 6 halfway across it. I conclude that silvered adults move completely about the habitat, and females probably oviposit in the mixed woods where host violets grow under conifers. But judging from the restricted distribution of unsilvered adults (Table 2), these are more local, and their restricted movement causes the habitat selection difference. In general, unsilvered Colorado adults prefer open woods with violets (N-facing slopes and gulch bottoms in the foothills), whereas silvered adults also occupy more open wet valley bottoms.

### *Pheromones*

Male odor of both forms from Mt. Judge was compared by the author. Males of silvered and unsilvered forms smelled the same: the odor is sweet but has a "hot" or "peppery" sensation, sweet but slightly peppery pungent. Virtually every male had this odor, a few weaker than others. Females lacked an odor. The description of odor is subjective, and different observers might use different words to describe it, but it was the same for both forms. Thus, the male pheromone is probably the same in both forms, although the human nose certainly cannot match the precision of laboratory instruments.

The pheromone system is complex. Males have androconial scales on dorsal wing veins (Scott 1986b:fig. 37) which evidently produce the pheromone odor; pheromone from these scales in the closely related European *Argynnis paphia* L. causes the female to land and accept the male (Magnus 1958). Females have a dorsal gland between abdomen segments 7 and 8 (Scott 1986b:fig. 37). This gland in *A. paphia* produces



a pheromone that attracts males: femalelike dummies attract males but do not elicit complete courtship, and freshly killed females are more attractive to males than dried females (Magnus 1958); virgins respond to nearby males by exposing the abdomen gland and aiming the abdomen tip toward the male (Treusch 1967). Males have a paired gland on the abdomen tip (Arnold & Fischer 1977, Scott 1986b) which, by comparison with *Heliconiini* (Scott 1986b), could possibly transfer pheromone to the female during mating to enable mated females to produce a third pheromone that repels males.

### *Courtship*

Courtship of *Speyeria atlantis*, which is nearly identical to that of *Argynnis paphia* (Magnus 1950), was described by Scott (1986b) based mainly on unsilvered form courtships in Jefferson Co., Colorado. In addition, a completed courtship between silvered male and female forms was seen at Mt. Judge: female on flower when male sighted her and landed; she fluttered her mostly spread wings with small amplitude for 1 s, he flicked his nearly closed wings behind her for 1–2 s; she rotated around flower top 1 revolution with her wings still spread while he rotated after her and flicked his nearly closed wings once during turn; she stopped, closed her wings, tilted forward so that her abdomen was raised slightly but lowered from between hindwings; he spread his wings partway; they joined.

Four courtships were seen at Mt. Judge between unsilvered males and silvered females, as follows.

1) Male patrolled near female (prior mating status unknown) on flower, landed, flicked wings (wingtips vibrating 0 to 1 cm apart about twice per s) for 10 s, curved abdomen laterally to attempt joining (meanwhile female, wings closed, leaned forward with abdomen lowered from between closed hindwings and abdomen raised above horizontal about 60°); wind blew them and he flew, fluttered over her for 1 s, landed, flicked beside her 10 s, curved his abdomen but was too close and his abdomen tip missed (during his bending she kept abdomen exposed), then he flew away. Female was evidently receptive because she exposed her abdomen and did not perform rejection dance (fluttering wings vigorously).

2) Male patrolled near silvered virgin (later found to have no spermatophores) on flower, landed, flicked his wings, she crawled away with closed wings, he crawled after her for 5 min while flicking and bending his abdomen, she stopped and spread wings partly while he flicked and curved abdomen to attempt mating for 5 min, he flew away (evidently she did not extrude genitalia, so he could not join). She was unreceptive even though she did not flutter her wings, perhaps because, as judged from weak flight, she was too young.

3) He pursued her in flight, they landed, she fluttered slightly and crawled away while he flicked his wings and crawled behind, she got farther away, he flew up a short distance but did not find her and flew away.

4) She raised her wings and slightly lowered and partly extruded her abdomen while he flicked his nearly closed wings behind her, he flew away after about 30 s.

Data on courtship between forms are too few to be conclusive, but no obvious courtship barriers to mating occur. Releases of reared virgins are needed. Grey et al. (1963) inconclusively report abnormal courtship of a few laboratory adults.

### *Larval Differences* (Figs. 1-14)

Color photographic slides were made of larvae and pupae from each study site except larvae from Corwina, and some larvae and pupae were preserved to correlate their color pattern with adult appearance.

From a distance, older larvae producing silvered adults (Figs. 5, 7-9) appear mottled black with orangish tan spines and two middorsal white lines, whereas older larvae producing unsilvered adults (Figs. 10-14) appear solid black with orange spines. Viewed more closely, larvae of both forms are basically black, with a pair of middorsal whitish lines 1 mm apart, and three rows of scoli (lateral to middorsal lines, suprspiracular, and subspiracular) which are tan or orange with black tips. The head of both forms is black with the dorsal half of the rear half of the head orangish.

Larvae of the silvered form (based on larvae from Tintytown, Figs. 5, 7-9) have the middorsal whitish lines conspicuous and mostly continuous, though alternately wider and narrower. Because Corwina pupae had less conspicuous lines than Tintytown pupae, Corwina larvae may not have had the lines this conspicuous. Scoli of the silvered form are orangish tan with black tips. Ground color is not as black as in the unsilvered form so three rows of black bands with very sinuous narrowly white edges are recognizable: along the dorsalmost scoli (edging middorsal white lines), along the suprspiracular scoli, and in between these (Figs. 8, 9). A light gray-brown transverse band circles the rear of each segment except middorsally, a remnant of the pale transverse stripes of *Speyeria nokomis* (Edw.) larvae (Scott & Mattoon 1981).

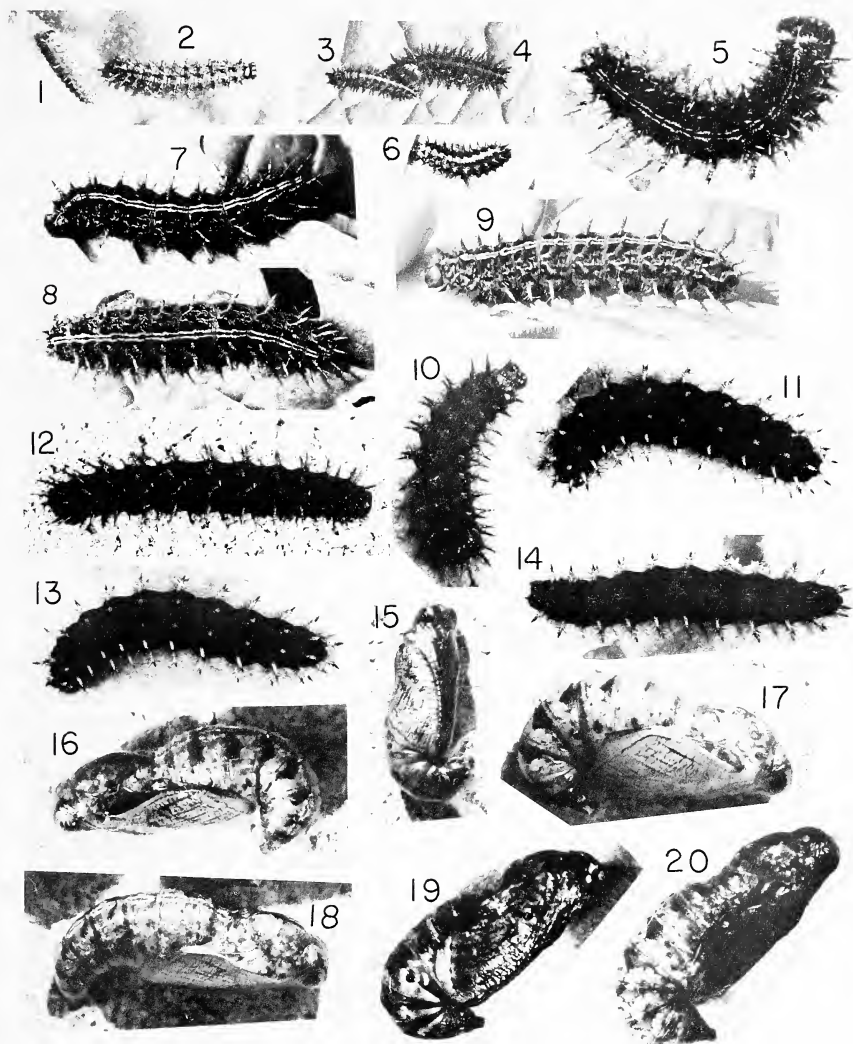
Larvae of the unsilvered form (from O'Fallon, Critchell, Cherry Gulch, Mt. Judge) are a little darker black and the pattern is obscured, so the black sinuous bands are unrecognizable without a microscope, and the middorsal two lines are fainter and broken into two dashed lines (Figs. 10-14). Scoli are orange with black tips. The only variation between localities among unsilvered larvae involves the single Cherry Creek larva which had slightly less orangish scoli. Edwards' (1888b) description of the unsilvered form is very similar.

The above descriptions of larvae do not correspond with descriptions of larvae of the silvered and unsilvered forms in the Black Hills of South Dakota (Grey et al. 1963). Both are described as identically black with orange spine shafts, the two middorsal lines grayish white in the unsilvered form, light brown in the silvered form. Thus the two middorsal lines are described as whiter in the unsilvered form in South Dakota, whereas they are whiter in the silvered form in Colorado. My descriptions are based on 104 larvae and dozens of color slides from many sites, whereas the South Dakota data are fewer.

Width of the two pale middorsal lines of the larva is apparently not closely linked to degree of silvering of the adult; among larvae producing silvered adults, the whiteness differed somewhat between the Tintytown and Corwina sites in Colorado as noted above, and differed between Colorado and South Dakota adults.

Thus, both larvae and adults of the unsilvered form have more pigment—more cream in adult scales, more orange on larval spines, more black on larval body—so one can guess that the gene responsible for the unsilvered form causes an increased deposition of some dark pigment such as melanin.

Larvae and pupae of silvered ventral-hindwing *S. atlantis* from NE



FIGS. 1-20. 1, First-stage larva, silvered form, Tinytown; 2, Second-stage larva, silvered form, Tinytown; 3, Third-stage larva, silvered form, Tinytown; 4, Fourth-stage larva, silvered form, Tinytown; 5, Fourth-stage larva, silvered form, Tinytown; 6, Third-stage larva, silvered form, Tinytown; 7, Mature larva, silvered form, Tinytown; 8, Mature larva, silvered form, Tinytown; 9, Mature larva, silvered form, Tinytown; 10, Third-stage larva, unsilvered form, O'Fallon female C; 11, Mature larva, unsilvered form, O'Fallon female C; 12, Mature larva, unsilvered form, Cherry Gulch; 13, Mature larva, unsilvered form, Mt. Judge female F; 14, Mature larva, unsilvered form, Mt. Judge female A; 15, Pupa (orange-brown wings), silvered form, Tinytown; 16, Pupa (orange-brown wings), silvered form, Tinytown; 17, Pupa (orange-brown wings), silvered form, Tinytown; 18, Pupa (orange-brown wings), silvered form, Tinytown; 19, Pupa (partly orange-brown wings), unsilvered form, O'Fallon female C; 20, Pupa (black wings), unsilvered form, Mt. Judge female F.



U.S. (Edwards 1888a) are grayer than Colorado-South Dakota *S. atlantis*; larvae and pupae evidently show geographic variation as do adults.

### *Pupal Differences*

(Figs. 15-20)

Pupae from localities with sufficient numbers show great individual variation, but there is no obvious important difference between silvered and unsilvered forms. The pupa resembles *S. nokomis* (Scott & Mattoon 1981) in general, but is darker (orange-brown), and the posterior half of each abdominal segment is darker because it is mottled with tiny black dots and dashes. The anterior half of each abdominal segment is not uniformly black as in *nokomis*: some pupae have a broad black irregular band, but most have the black areas broken into spots, including triangular spots just beside the anterior-pointing orange-brown middorsal triangles on segments 5-7. Pupae from Tynytown have two sinuous tan middorsal abdominal lines, but pupae from Corwina (both sites produced silvered adults) and the other sites had weak tan middorsal lines. Pupal wing color varies from mostly black to almost wholly orange-brown, but most are mostly orange-brown, a few black-winged.

Grey et al. (1963) describe the pupal wing cases of silvered forms as darker with less light brown mottling than those of unsilvered forms in the Black Hills. However, they reared only three silvered adults, so the difference is probably due to small sample size because all Colorado sites with large samples show considerable variation in pupal wing color. Pupae producing silvered adults are not darker in Colorado.

### DISCUSSION

There are several reasons why *S. a. atlantis* and *S. a. hesperis* could be treated as distinct species: they often fly together, they prefer different microhabitats, amount of silvering seems usually linked with ventral hindwing color, mothers usually produce offspring resembling themselves, and their larvae differ. If scientists were aware only of Black Hills populations, the two would certainly be treated as separate species because they are so distinct there. Some anecdotes (coincidences?) also fit the two-species theory. For instance, six unsilvered males and one silvered pair were found in the Mt. Judge mixed woods 28 July 1987, the silvered pair in copula.

There are several reasons why *S. a. atlantis* and *S. a. hesperis* could be treated as one species:

- 1) Silvered and unsilvered forms are linked by a complete series of intermediate adults, from slightly to partly to half to mostly silvered, although only slightly silvered intermediates are common.

2) Unsilvered mothers sometimes produce silvered offspring (Grey et al. 1963:146), and half-silvered mothers often produce unsilvered offspring (Table 1).

3) In many populations, silvered forms are rare (<5%) as in the lower foothills of the Colorado Front Range, rarely a true species might have difficulty surviving. The reverse is also true, in which unsilvered forms are rare within silvered populations, as in the wet center of the Black Hills (Grey et al. 1963). However, *S. coronis* (Behr) is just as rare and it survives.

4) Frequencies of the forms show clinal trends, both altitudinally in the Colorado Front Range, and along habitat gradients. For instance, in the Black Hills (Grey et al. 1963), *atlantis* is common in wet meadow habitats on poorly drained granite, and is rarer away from these areas. Similarly, in S Colorado (Scott & Scott 1980) *hesperis* predominates in the lower foothills, both forms occur in dry areas at higher altitude, and *atlantis* predominates in three wet meadow enclave habitats at middle altitudes: Coaldale in Arkansas Canyon, Fremont Co.; SW of Westcliffe on Wet Mountain Valley floor, Custer Co.; Stonewall in upper Purgatoire River valley, Las Animas Co. Such enclaves have not been found in the Front Range W of Denver, where silvered forms are rare in the foothills and increase in frequency with altitude until they predominate in the upper Canadian Zone.

5) When attempts are made to divide *S. atlantis* into silvered and unsilvered "species", their distributions are incongruous because unsilvered forms cut an E-W swath through the range of silvered forms, replacing them in the process (Scott 1986b).

The silvered-unsilvered division also fails to solve the problem of sympatry of *S. a. dennisi* and *S. a. atlantis (hollandi)*, both of which are silvered, in Manitoba. A species *S. dennisi* could include *S. atlantis ratonensis* Scott from NE New Mexico and *S. a. greyi* from NE Nevada, but *dennisi* is said to intergrade W to *atlantis* in Saskatchewan-Alberta, and *greyi* intergrades with *dodgei* in S Idaho (P. C. Hammond pers. comm.), and at least *greyi* seems independently evolved toward similar pallidity.

6) Other *S. atlantis* subspecies have polymorphisms of silvered-unsilvered adults: *wasatchia* dosP. & G. (= *tetonia* dosP. & G.) in W Wyoming-Utah is usually unsilvered, *chitone* (Edw.) in S Utah and *schellbachii* Garth in N Arizona are usually silvered.

7) Other species of *Speyeria* have silvered-unsilvered polymorphisms: *zerene* (Bdv.) in California and S Oregon, *callippe* (Bdv.) in N California and the Sierra Nevada, *egleis* (Behr) in the Sierra and Utah, *hydaspe* (Bdv.) in British Columbia. These polymorphisms are accepted by lepidopterists. Boggs (1987) hypothesized that rare unsilvered *S. mormonia* are homozygous recessives that fail to reproduce, which is dubious because *S. mormonia artonis* (Edw.) are nearly always unsilvered.

8) Association between ventral hindwing color and silvering and larval color pattern breaks down geographically. In the Black Hills and E of the continental divide in the Colorado mountains, silvered adults have a chocolate-brown ventral hindwing (darker in the Black Hills), and unsilvered adults usually have a reddish brown ventral hindwing. However, in N-central New Mexico, 98% of adults (N = 60) are silvered but the ventral hindwing varies from chocolate- to reddish brown. In SW Manitoba *S. atlantis dennisi* and *S. a. atlantis (a. hollandi)* are 100% silvered but the ventral hindwing is usually light brown in the former and chocolate-brown in the latter. And silvered adults have the ventral hindwing browner in the Black Hills than in the Colorado Front Range. Larval differences in Colorado are partially reversed in the Black Hills, and larvae are grayer in E North America.

The conclusion that silvered and unsilvered adults are polymorphic forms of one species seems preferable.

### Paleogeography

The current geographic distribution of wing characters suggests that the dark silvered form (*S. a. atlantis*) occupied the coniferous forest in N U.S. and the Rocky Mountain foothills during the Ice Age; afterwards

it moved higher in altitude and latitude. The unsilvered form with reddish brown ventral hindwing (now *S. a. hesperis*, *a. wasatchia*, *a. irene* [Bdv.]) occupied open forest in the southern Great Basin lowlands; after the Ice Age it spread N into the mountains, E through lowland S Wyoming to the Black Hills, and S along the Colorado mountain foothills. The silvered form with narrower black lines and a pale brown ventral hindwing (now *S. atlantis dennisi* and *a. ratonensis*) occupied aspen parkland in the current S Great Plains or central Texas; after the Ice Age it spread, respectively, N to Canada, and upward to a mountain mesa. The forms became sympatric after the Ice Age.

### Mechanism of Inheritance

The inheritance mechanism of silvering is unknown. Rarity of half-silvered adults suggests dominance, but some broods with half the offspring silvered and half unsilvered should occur but did not. If half-silvered adults were heterozygotes, they would not produce all-unsilvered broods as at Critchell. If silvered is dominant, rare silvered mothers would be likely to produce silvered offspring, as at Tinytown and Corwina. O'Fallon and Cherry Gulch broods perhaps suggest modifier genes that cause part-silvering.

Maternal inheritance seems the best guess now, and fits all the reared broods; offspring would resemble the mother, the father having no effect or perhaps merely modifying partly silvered offspring. Sterling O. Mattoon (pers. comm.) states that *Speyeria* offspring generally resemble their mother very closely, although some silvered offspring have been reared from unsilvered mothers and vice versa.

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POPULATION FLUCTUATIONS OF  
*AZETA VERSICOLOR* (FABRICIUS) (NOCTUIDAE)  
ON *GLIRICIDIA SEPIUM* (JACQ.) (FABACEAE)  
IN NORTHEASTERN COSTA RICA

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**ABSTRACT.** Counts of early stages, especially caterpillars, of *Azeta versicolor* on the host tree *Gliricidia sepium* planted as shade cover in a vanilla plantation were made intermittently during five years. Based on field observations and rearings, the mature caterpillar and pupa were described, noting two distinct color morphs in the former. Tachinid parasites were also noted. Caterpillar abundance was analyzed and interpreted in relation to monthly rainfall and leaf-flushing in the host tree, since caterpillars feed preferentially on new (flush) leaves. Numbers of caterpillars were highly correlated with monthly rainfall. It is concluded that population cycles of the moth are regulated by seasonal patterns of leaf-flushing in the host.

**Additional key words:** immature stages, leaf flushing, population dynamics.

Impact of seasonal fluctuations in rainfall on leaf-flushing of semi or fully deciduous host trees is a major environmental factor molding population dynamics of noctuids and other Lepidoptera in the tropics (Vaishampayan & Veda 1980, Blair 1982, Tucker & Pedgley 1983). Fabaceous legume crops in the tropics are especially preferred hosts of noctuid and pyralid defoliators, with seasonal patterns of population outbreaks typical for several of these host species (Bradley & Carter 1982, Panchabhavi & Holihosur 1982). In many species, caterpillars preferentially defoliate immature leaves or other most nutritious tissues of the host, which are often only seasonally available (Futuyma & Wasserman 1980, Bracken 1984). Here I report seasonal abundance pattern of immature stages for the noctuid moth *Azeta versicolor* (Fabricius) on leaves of the fabaceous legume tree *Gliricidia sepium* (Jacq.) planted as shade cover in a vanilla plantation.

METHODS

Counts of life stages of *Azeta versicolor* were obtained on 16 dates between March 1982 and June 1987 at "Finca La Tirimbina," near La Virgen (10°23'N; 84°07'W; 200 m elev.), Sarapiquí District, Heredia Province. Within a ca. 1600 m<sup>2</sup> plot containing about 900 trees of *Gliricidia sepium* planted a few years earlier to shade vanilla plants, 30 arbitrarily selected trees (canopy height ca. 3 m) were censused for *Azeta versicolor* caterpillars at various times. The medium-sized (40 mm wingspan) adults and caterpillars were readily recognizable in field censuses: adult moths are drab greenish brown with striking red ab-

dominal coloration, and yellowish mature caterpillars usually rest close to the base of host trees, typically on stems and leaves of vanilla orchid vines and other epiphytes under the trees.

On a given caterpillar census, as many as 100 samples of both mature or immature leaves and stems on each tree (usually up to height of 1.5 m) were searched for "young" caterpillars (mixed early instars) and eggs. Condition of canopy foliage of *Gliricidia sepium* was also noted (such as presence or absence of flush leaves), providing a qualitative picture of local timing of peak flushing periods in relation to seasonality. A total of 30 caterpillars (later instars) were placed in clear-plastic bags containing fresh cuttings of *G. sepium* and kept tightly shut for rearing. Parasitism of caterpillars and pupae was noted from this sample.

## RESULTS

**Natural history.** In both of two color morphs of the final stage caterpillar, roughly equal in abundance and not sexual dimorphism, the head is pinkish white with black dots. Thoracic and abdominal regions of the mature caterpillar (40 mm long by 5 mm wide) have eight lengthwise narrow bands, which, in the dark form are as follows, dorso medial to latero ventral: (1) deep yellow; (2) faintly yellow edged in black; (3) pale bluish streaked with tiny black lines and a single round black dot on each segment; (4) pale bluish yellow; (5) wide pale blue; (6) lateral (spiracular) stripe pale blue with thin black line medially and reddish spiracle openings, each with a black dot dorsoanteriorly and yellow dot ventroposteriorly; (7) yellow with black edging ventrally; (8) grayish with raised black dot, one per segment. Prolegs pinkish, each with yellow dot laterally, ringed with black. Glossy black elongate setae on profuse raised areas of cuticle. Anal clasper faintly pinkish; true legs reddish. In the light form, there are no black stripes bordering other stripes.

The reddish brown pupa (20–22 mm long by 5–6 mm wide) occurs in a loosely constructed cocoon of host leaves pulled together and anchored with light brown silk. Both caterpillar and pupa thrash about vigorously when picked up. Adults are active throughout the day, and are skittish and difficult to capture with an insect net. The spherical, glossy yellow eggs are placed singly on the undersides of *G. sepium* leaves. Of 257 eggs discovered in the field, ca. 70% were on immature (meristem) leaves. As noted above, mature caterpillars rest on vanilla vines and other epiphytic debris on host trunks during daytime, and are chiefly nocturnal feeders, crawling into the *G. sepium* canopy to feed. Each of 3 pupae (out of 30 reared from collected caterpillars) yielded 1 tachinid parasite.



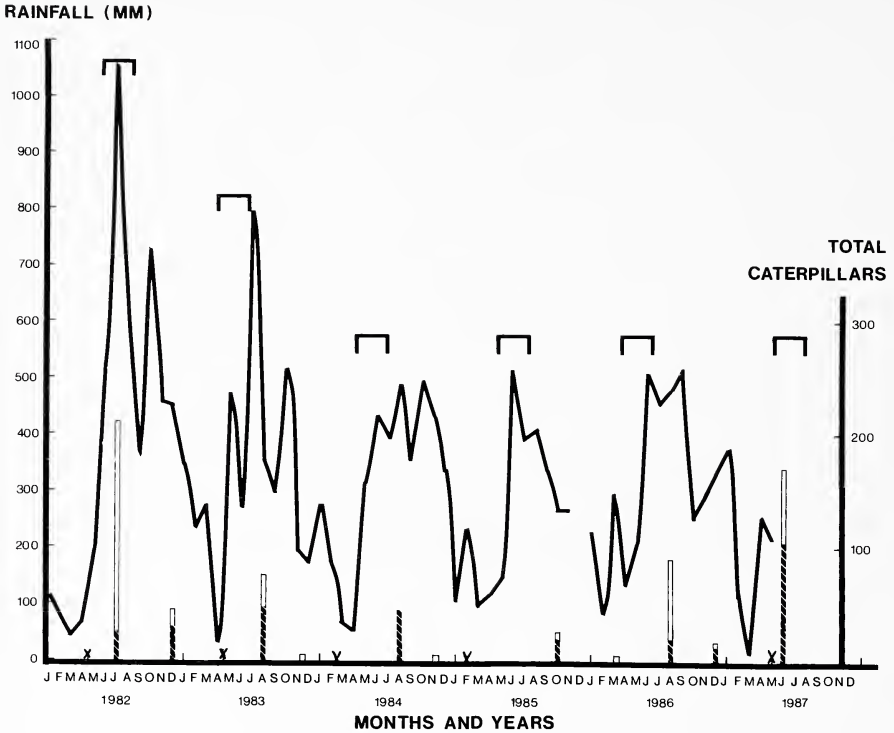


FIG. 1. Monthly total rainfall (line), total numbers of *Azeta versicolor* caterpillars (vertical bars, 5th instars represented by hatching), timing of leaf-flushing (brackets), and periods of caterpillar absences (x), in the 36-tree subplot of *Gliricidia sepium* at "Finca La Tirimbina." Rainfall data courtesy of Finca La Tirimbina.

**Seasonal population fluctuations and leaf-flushing.** Abundance of *Azeta versicolor* caterpillars on sampled *Gliricidia sepium* trees varied greatly among census dates (Fig. 1). Aside from an occasional hesperiid and limacodid caterpillar, I did not observe other herbivores abundant on these trees. When the data are examined relative to rainy and dry season periods at La Tirimbina, two patterns become apparent: (1) the highest numbers of mature and partly grown caterpillars occurred in the rainy season, especially June–August, approximately during the first half of the lengthy rainy season characteristic of this locality; (2) caterpillars are absent during the dry season (February–March) (Fig. 1). A high positive correlation resulted between numbers of caterpillars and monthly rainfall ( $r = 0.81$ ,  $P < 0.01$ ).

Also during July–August, as many as 500 adults were counted within a 600 m<sup>2</sup> strip of low vegetation bordering one side of the vanilla grove during a 2 morning census (0800–1000 h). As many as 100 eggs were counted within the 36-tree subplot on a single day in July or August,

and none were found in February or March. During dry months, host trees are partly deciduous, and only mature leaves are present. Flowering in *G. sepium* at La Tirimbina is most intense during March and early April. During the first three months of the rainy season, *G. sepium* exhibits intensive leaf flushing (Fig. 1).

The highest population density of *Azeta versicolor* at La Tirimbina follows intense flushing of new leaves on larval host trees. The increased availability of immature (flush) leaves during the beginning of the rainy season provides an abundant food resource for larvae. Population build-up can be so intense in the rainy season as to result in 80–100% defoliation of *G. sepium* on some plots. I conclude that the breeding population of this Neotropical noctuid fluctuates in size throughout the year at La Tirimbina in a consistent manner, and in response to the seasonal leaf-flushing cycle of *G. sepium*.

#### DISCUSSION

Some tropical legume crops attacked by host-specific noctuids and other moths undergo severe defoliation at certain times of year (Singh & Budhraj 1980). Legume tree species typically planted as a permanent shade over perennial crops in the tropics such as cacao, coffee, and vanilla, including *G. sepium* (Inostrosa & Fournier 1982), and others such as *Erythrina* (Borchert 1980) undergo pronounced seasonal cycles in leaf-flushing in direct response to water-stress and rehydration (Reich & Borchert 1982). The complete absence of *Azeta versicolor* caterpillars on *Gliricidia sepium* in the dry season at La Tirimbina is due to absence of immature (newly flushed) leaves. Thus, availability of edible leaf tissues, a consequence of seasonally regulated hostplant leaf-flushing, determines temporal pattern of population build-up in this noctuid. The degree to which *A. versicolor* exploits other larval host plants at La Tirimbina is unknown.

Skittish behavior of the diurnally active adults, and their vivid red abdominal colors, suggest aposematism, perhaps a consequence of larval feeding on *G. sepium*, a species well known for high concentrations of coumarin compounds in its leaves (Allen & Allen 1981). Marked build-up of the adult population in the first half of the rainy season at La Tirimbina suggests a population structure in which biotic regulation of the herbivore may be minimal.

*Gliricidia sepium* is capable of producing a new flush of leaves following a period of intense herbivory by (J. R. Hunter & A. M. Young pers. obs.). The ability of *G. sepium* to recover rapidly from intense defoliation may be mediated in large part by the tree's capacity to fix nitrogen in the soil.

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## BUTTERFLIES OF NORTHEAST TENNESSEE

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**ABSTRACT.** Here we give results of a 10-year survey of butterflies in a seven-county, 7000 km<sup>2</sup> area of NE Tennessee. Ninety-one species are listed and their seasonal occurrence tabulated on a 10-day basis. Twenty-seven species are judged to be univoltine, twenty-nine bivoltine, and twenty-one multivoltine. The remainder are thought to be migrants or strays that do not overwinter in NE Tennessee. Comparison of our species list with that of SW Virginia and N Georgia indicates the fauna lacks a number of lowland species that occur in N Georgia, and some typically northern species in SW Virginia. Ten species known to occur in both comparison areas, but not recorded here, will probably be found in the future.

**Additional key words:** Appalachians, biogeography, survey, Georgia, Virginia.

There is little published information on the butterfly fauna of Tennessee (Field et al. 1974). Osburn (1895a, 1895b) lists 70 species occurring around Nashville. Richards (1932) provides some Tennessee records. Watson (1946) and Snyder (1957) list some species occurring in the Smoky Mountains. The best source for the State as a whole is Opler (1983) which contains county distribution maps for all species occurring in the eastern U.S.

We have collected extensively in NE Tennessee for more than 10 years. Here we summarize results of our collecting, make comparisons with other areas in the S Appalachian region, and list additional species likely to occur in NE Tennessee.

### STUDY AREA

The area encompasses seven counties in NE Tennessee with a total area of 7000 km<sup>2</sup> (Fig. 1). Two physiographic subdivisions of the S Appalachian region are represented. The SE portion of the area lies within the Blue Ridge Province, the remainder in the Ridge and Valley Province.

The peaks of the Blue Ridge are known locally as the Unaka Mountains. They are characterized by rugged terrain and heavily forested slopes. Elevations vary from 450-600 m in the narrow valleys to 750-1900 m on the peaks. Underlying sedimentary and metamorphic rocks are Cambrian and Pre-Cambrian in age. Soils tend to be sandy and acidic. Most of this portion of the area lies within the Cherokee National Forest (Miller 1974, USDA 1953, 1956, 1985).

The Ridge and Valley portion is underlain by strongly folded sedimentary rocks of Ordovician and Cambrian age. Differential weathering has resulted in long, narrow sandstone ridges trending NE to SW, alternating with valleys developed on less resistant limestone and shale. The easternmost valley is broad and part of a series of connecting valleys extending from Pennsylvania to Alabama commonly called the Great Valley.

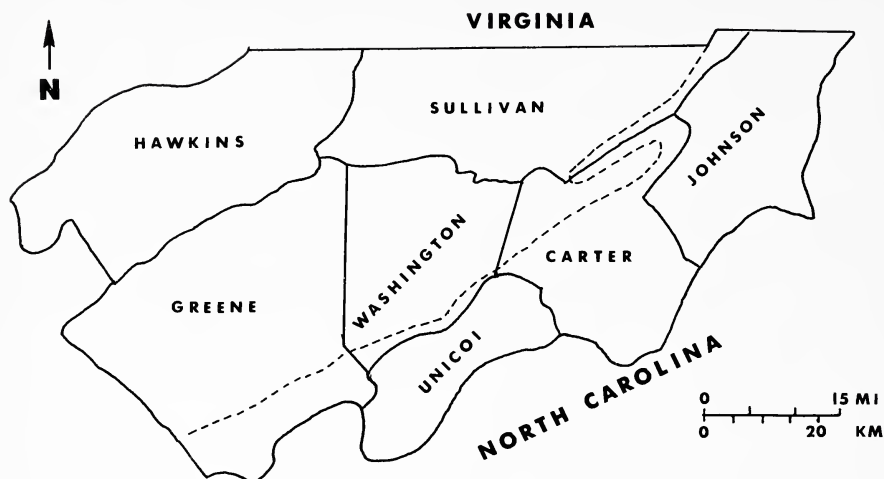


FIG. 1. Study area in NE Tennessee, showing county boundaries. Dashed line is approximate boundary separating Blue Ridge Province (Unaka Mts., SE) from Ridge and Valley Province (NW).

Within it there is local relief in the form of shale knobs and entrenched streams. To the NW, straddling the border of Greene and Hawkins counties, and extending into SW Sullivan Co., are a group of ridges collectively called Bays Mountain. Another prominent feature, Clinch Mountain, runs through NW Hawkins Co. Elevations average lower in the Ridge and Valley Province, ranging from 300 m in the valleys to 600–900 m on ridges. Ridge soils are generally sandy, shallow, and unproductive while valley soils developed on limestone are rich and fertile (Fenneman 1938, Miller 1974, U.S. Dep. Agric. 1953b, 1958a, 1958b, 1979, 1985).

The entire area is drained by the Holston River and its tributaries, part of the Tennessee River drainage system. The rivers have been extensively impounded for flood control and power generation (Hunt 1967).

Climate is characterized by mild winters and warm summers. Average annual precipitation is 100–150 cm except at highest elevations where it may exceed 200 cm. Topography and altitudinal differences cause much local variation in climate. As a rule, S- and W-facing slopes are drier than those facing N and E. Average frost-free season varies from 190 days in NW valleys to 150 days in the Unaka mountains (Walker 1969, U.S. Dep. Agric. 1953, 1979).

Before European settlement, the area was covered with oak-chestnut forest. Clearing of valleys for agriculture, logging in the mountains, and chestnut blight decimated primary forests, especially in the Ridge and Valley. Today forests are concentrated in the Unaka Mountains and on the NW ridges. At lower elevations, oaks (*Quercus* spp.), hickories (*Carya* spp.), yellow poplar (*Liriodendron tulipifera* L.) and other hardwoods are common, often mixed with hemlock (*Tsuga* spp.), and several pines (*Pinus* spp.). The Unaka Mountains are high enough to show altitudinal zonation. Above 900 m, northern forest types such as sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britton) are common. Above 1500 m, red spruce (*Picea rubens* Sarg.), and fraser fir (*Abies fraseri* [Pursh.] Poir) predominate. Treeless, dome-shaped summits called balds occur on some peaks. In the Ridge and Valley, stands of red cedar (*Juniperus virginiana* L.) are common in old fields on limestone soils. Marshes and canebrakes are rare throughout, most having been drained, cleared, or inundated by reservoirs (Braun 1950, Walker 1969, U.S. Dep. Agric. 1953a, 1953b, 1956, 1958a, 1958b, 1979, 1985).

## METHODS

Most records come from collections and fields notes made by the authors from 1975 through 1986. Additional records were obtained from participants in a Southern Lepidopterist Society field meeting in the area in 1980, and from collections made by students at Sullivan (County) High School during fall 1977 and 1978. Collections at the U.S. National Museum (USNM) and the Carnegie Museum of Natural History (CMNH) were examined, but no additional records were found. Most specimens are retained in the authors' collections; others have been placed in USNM and CMNH. Some identifications were confirmed by C. V. Covell Jr., University of Louisville, and by R. K. Robbins and J. M. Burns (USNM). Butterfly nomenclature follows Hodges et al. (1983).

To facilitate comparison with NE Tennessee, we define SW Virginia as Giles, Montgomery, and Floyd counties and those counties to the SW entirely or predominantly within the transition zone of Clark and Clark (1951). North Georgia is defined as those counties entirely or predominantly within the mountain region of the State as defined by Harris (1972). Species records for these regions were obtained from Opler (1983), Clark and Clark (1951), and Harris (1972).

## RESULTS AND DISCUSSION

We recorded 91 species of butterflies and skippers from NE Tennessee (Table 1). In addition, specimens of *Celastrina ladon* form *neglecta-major* Tutt, considered by some to be a distinct species (Opler & Krizek 1984), have been collected in May and early June. An old sight record for *Anaea andria* Scudder for which we do not have a precise date is not included in the table but is discussed below.

The species found in NE Tennessee can be considered as falling into two categories: residents, which overwinter in the area; and migrants or strays, which do not normally overwinter in the area, although many regularly occur in summer and fall.

A number of resident species are rare or local in distribution, but only one appears limited to a particular part of the study area. *Speyeria aphrodite* (F.) has been collected only in the Blue Ridge, where it is often common at elevations above 600 m.

Analysis of flight-period data in Table 1 to determine number of broods for resident species is complicated by the fact that the flight period of a species at any particular locality may vary from year to year due to climatic and biological factors. Flight periods are also affected by elevation, beginning and ending one to three weeks later at high elevations in the Blue Ridge than in the Ridge and Valley. For example, summer brood *Erynnis horatius* (Scudder & Burgess) has been collected at Bays Mountain Park (600 m) in Sullivan Co. from late June through mid-August, but a fresh specimen was collected in Carter Co. at 1200 m on 8 September.

We believe the following residents are univoltine in NE Tennessee:

*Thorybes bathyllus* (J. E. Smith)

*T. pylades* (Scudder)

*Erynnis icelus* (Scudder & Burgess)

*E. brizo* (Bdv. & Leconte)

*E. juvenalis* (F.)

*Wallengrenia egremet* (Scudder)

TABLE 1. Temporal distribution of butterfly species adults in NE Tennessee.

Species	Mar.		Apr.			May		
	11- 20	21- 31	1- 10	11- 20	21- 30	1- 10	11- 20	21- 31
<b>Hesperiidae</b>								
<i>Epargyreus clarus</i>				X	X	X	X	X
<i>Autochthon cellus</i>								X
<i>Achalarus lyciades</i>								X
<i>Thorybes bathyllus</i>								
<i>T. pylades</i>								X
<i>Staphylus hayhurstii</i>								
<i>Erynnis icelus</i>				X	X	X		
<i>E. brizo</i>			X	X	X			
<i>E. juvenalis</i>			X	X	X	X	X	X
<i>E. horatius</i>								
<i>E. baptisiae</i>								
<i>Pyrgus communis</i>					X			
<i>Pholisora catullus</i>								
<i>Nastra lherminier</i>								X
<i>Ancyloxypha numitor</i>								X
<i>Thymelicus lineola</i>								
<i>Hylephila phyleus</i>								
<i>Polites coras</i>							X	X
<i>P. themistocles</i>								X
<i>P. origenes</i>						X		
<i>Wallengrenia egeremet</i>								
<i>Pompeius verna</i>							X	X
<i>Atalopedes campestris</i>								X
<i>Atrytone delaware</i>								X
<i>Poanes hobomok</i>							X	X
<i>P. zabulon</i>					X	X	X	X
<i>Euphyes ruricola metacomet</i>								X
<i>Amblyscirtes hegon</i>					X		X	
<i>A. aesculapius</i>							X	X
<i>A. vialis</i>				X		X		
<b>Papilionidae</b>								
<i>Battus philenor</i>			X	X	X	X	X	X
<i>Papilio polyxenes asterius</i>			X		X	X	X	
<i>P. cresphontes</i>								
<i>P. glaucus</i>		X	X	X	X	X	X	X
<i>P. troilus</i>			X	X	X	X	X	X
<i>Eurytides marcellus</i>		X	X	X	X	X	X	X
<b>Pieridae</b>								
<i>Pontia protodice</i>								
<i>Artogeia virginiensis</i>			X	X	X	X	X	X
<i>A. rapae</i>	X	X	X	X		X	X	X
<i>Euchloe olympia</i>		X	X	X		X		
<i>Falcapica midea</i>		X	X	X	X	X	X	
<i>Colias philodice</i>	X		X	X	X	X		X
<i>C. eurytheme</i>	X	X	X	X	X		X	
<i>Phoebis sennae eubule</i>								
<i>Eurema lisa</i>								
<i>E. nicippe</i>								









TABLE 1. Continued.

Species	Mar.		Apr.			May		
	11- 20	21- 31	1- 10	11- 20	21- 30	1- 10	11- 20	21- 31
<b>Lycaenidae</b>								
<i>Feniseca tarquinius</i>						X		
<i>Lycaena phlaeas americana</i>					X	X		
<i>Harkenclenus titus mopsus</i>								
<i>Satyrrium calanus falacer</i>								X
<i>S. caryaevorum</i>								
<i>S. liparops strigosum</i>								
<i>Calycopis cecrops</i>					X		X	
<i>Mitoura grynea</i>					X	X	X	
<i>Incisalia augustus croesioides</i>				X				
<i>I. henrici</i>		X	X	X	X	X	X	
<i>I. niphon</i>		X	X	X	X	X	X	
<i>Parrhasius m-album</i>								
<i>Strymon melinus</i>			X	X	X	X		
<i>Erora laeta</i>				X	X	X		
<i>Everes comyntas</i>			X	X	X	X		
<i>Celastrina ladon</i>		X	X	X	X		X	X
<i>C. ebenina</i>				X	X	X		
<i>Glaucopsyche lygdamus</i>				X	X	X		
<b>Libytheidae</b>								
<i>Libytheana bachmanii</i>								
<b>Nymphalidae</b>								
<i>Polygonia interrogationis</i>	X					X		X
<i>P. comma</i>	X	X	X					X
<i>Nymphalis antiopa</i>	X	X	X	X	X	X		X
<i>Vanessa virginiensis</i>				X	X		X	
<i>V. cardui</i>						X		
<i>V. atalanta</i>								X
<i>Junonia evarete</i>								
<i>Euptoieta claudia</i>								
<i>Speyeria diana</i>								
<i>S. cybele</i>						X		X
<i>S. aphrodite</i>								
<i>Clossiana bellona toddi</i>			X	X	X	X		X
<i>Phyciodes tharos</i>					X	X	X	X
<i>Charidryas nycteis</i>							X	X
<i>Euphydryas phaeton</i>								
<i>Basilarchia arthemis astyanax</i>								X
<i>B. archippus</i>								X
<b>Apaturidae</b>								
<i>Asterocampa celtis</i>							X	X
<i>A. clyton</i>								X
<b>Satyridae</b>								
<i>Enodia anthedon</i>								X
<i>E. creola</i>								
<i>Cyllopsis gemma</i>				X		X	X	
<i>Hermeuptychia sosybius</i>								X
<i>Megisto cymela</i>								X
<i>Cercyonis pegala</i>								
<b>Danaidae</b>								
<i>Danaus plexippus</i>					X			



TABLE 1. Continued.

[illegible]



TABLE 1. Continued

Species	Mar			Apr			May		
	11-20	21-31	1-10	11-20	21-30		1-10	11-20	21-31
<b>Lycaenidae</b>									
<i>Feenisea tarquinius</i>							X		
<i>Lycaena phlaeas americana</i>						X	X		
<i>Harknessulus titus mopsus</i>									
<i>Satyrion calanus falacer</i>									X
<i>S. caryacorum</i>									
<i>S. liparops strigosum</i>									
<i>Calycopis cecrops</i>						X		X	
<i>Mitoura grynea</i>						X	X	X	
<i>Icthisalia augustus croceoides</i>				X					
<i>I. henrici</i>		X	X	X	X	X	X	X	
<i>I. niphon</i>		X	X	X	X	X		X	
<i>Parthassius n-album</i>									
<i>Strymon melinus</i>			X	X	X	X			
<i>Erora laeta</i>				X	X	X			
<i>Eceres comyntas</i>			X	X	X	X			
<i>Celastrina ladon</i>		X	X	X	X			X	X
<i>C. ebenina</i>				X	X	X			
<i>Glaucopsyche lygdamus</i>				X	X	X			
<b>Libytheidae</b>									
<i>Libytheana bachmanii</i>									
<b>Nymphalidae</b>									
<i>Polygonia interrogationis</i>	X						X		X
<i>P. comma</i>	X	X	X						X
<i>Nymphalis antiopa</i>	X	X	X	X	X	X	X		X
<i>Vanessa virginensis</i>				X	X			X	
<i>V. cardui</i>							X		
<i>V. atalanta</i>									X
<i>Junonia crearte</i>									
<i>Euptoieta claudia</i>									
<i>Speyeria diana</i>									
<i>S. cybele</i>							X		X
<i>S. aphrodite</i>									
<i>Clossiana bellona toddi</i>			X	X	X	X	X		X
<i>Phyciodes tharos</i>					X	X		X	X
<i>Charidryas nycteis</i>								X	X
<i>Euphydryas phacton</i>									
<i>Basilarchia arthemis astyanax</i>									X
<i>B. archippus</i>									X
<b>Apaturidae</b>									
<i>Asterocampa celtis</i>								X	X
<i>A. clyton</i>									X
<b>Satyridae</b>									
<i>Enodia anthedon</i>									X
<i>E. creola</i>									
<i>Cyllopsis gemma</i>					X		X	X	
<i>Hermecryptychia sosylnus</i>									X
<i>Megisto cymela</i>									X
<i>Cercyonis pegala</i>									
<b>Danaidae</b>									
<i>Danaus plexippus</i>						X			

TABLE 1. Continued

[illegible]

*Poanes hobomok* (Harr.)  
*Euphyes ruricola metacomet* (Harr.)  
*Amblyscirtes hegon* (Scudder)  
*Artogeia virginienensis* (Edw.)  
*Euchloe olympia* (Edw.)  
*Falcapica midea* (Hbn.)  
*Harknclenus titus mopsus* (Hbn.)  
*Satyrrium calanus falacer* (Godt.)  
*S. caryaevorum* (McD.)  
*S. liparops strigosum* (Harr.)

*Incisalia augustus croesioides* (Scudder)  
*I. henrici* (G. & R.)  
*I. niphon* (G. & R.)  
*Celastrina ebenina* Clench  
*Glaucoopsyche lygdamus* (Doubleday)  
*Speyeria diana* (Cram.)  
*S. aphrodite*  
*Euphydryas phaeton* (Drury)  
*Megisto cymela* (Cram.)  
*Cercyonis pegala* (F.)

*Speyeria cybele* (F.) flies from May through September and would appear to be multivoltine, but the long flight period is caused by staggered emergence of a single brood (Opler & Krizek 1984, Scott 1986).

The following are bivoltine:

*Autochon cellus* (Bdv. & Leconte)  
*Achalarus lyciades* (Gey.)  
*Nastra lherminier* (Latr.)  
*Polites coras* (Cram.)  
*P. themistocles* (Latr.)  
*P. origenes* (F.)  
*Pompeius verna* (Edw.)  
*Atrytone delaware* (Edw.)  
*Poanes zabulon* (Bdv. & Leconte)  
*Lycaena phleas americana* (Harr.)  
*Calycopis cecrops* (F.)

*Mitoura grynea* (Hbn.)  
*Nymphalis antiopa* (L.)  
*Charidryas nycteis* (Doubleday)  
*Basilarchia arthemis astyanax* (F.)  
*B. archippus* (Cram.)  
*Asterocampa celtis* (Bdv. & Leconte)  
*A. clyton* (Bdv. & Leconte)  
*Enodia anthedon* A. H. Clark  
*E. creola* (Skin.)  
*Cyllopsis gemma* (Hbn.)  
*Hermeuptychia sosybius* (F.)

Fresh *Basilarchia archippus* and *B. arthemis astyanax* taken in October and early November indicate that partial third broods are produced when mild weather persists well into fall.

Additional species are probably bivoltine, though not apparent from our data. *Erynnis horatius* (Scudder & Burgess) and *E. baptisae* (Fbs.) should have spring broods on the wing in April and May. They have likely been overlooked amid large numbers of *E. juvenalis* flying at that time. *Pholisora catullus* (F.) is also likely to have a spring brood, and is probably more common than our records suggest. *Erora laeta* (Edw.), *Amblyscirtes aesculapius* (F.), *A. vialis* (Edw.), and *Staphylus hayhurstii* (Edw.) have been taken only in spring or early summer. All four species probably have second broods in summer overlooked due to very local occurrence.

Another group of resident species are multivoltine, with three or more broods per year:

*Epargyreus clarus* (Cram.)  
*Ancyloxypha numitor* (F.)  
*Battus philenor* (L.)  
*Papilio polyxenes asterius* Stoll  
*P. glaucus* L.  
*P. troilus* L.  
*Eurytides marcellus* (Cram.)

*Artogeia rapae* (L.)  
*Colias philodice* Godt.  
*C. eurytheme* Bdv.  
*Feniseca tarquinius* (F.)  
*Strymon melinus* Hbn.  
*Everes comyntas* (Godt.)  
*Celastrina ladon* (Cram.)



*Polygonia interrogationis* (F.)  
*P. comma* (Harr.)  
*Vanessa virginiensis* (Drury)

*V. atalanta* (L.)  
*Clossiana bellona toddi* (Holl.)  
*Phyciodes tharos* (Drury)

One additional species, *Parrhasius m-album* (Bdv. & Leconte), is probably multiple brooded. We have taken a worn specimen in SW Virginia near the Tennessee line in early May, and sources indicate that a third brood in late August–September is likely (Opler & Krizek 1984, Scott 1986).

We consider the following species to be migrants or strays:

*Pyrgus communis* (Grt.)  
*Hylephila phyleus* (Drury)  
*Atalopedes campestris* (Bdv.)  
*Papilio cresphontes* (Cram.)  
*Pontia protodice* (Bdv. & Leconte)  
*Phoebis sennae eubule* (L.)  
*Eurema lisa* (Bdv. & Leconte)

*E. nicippe* (Cram.)  
*Libytheana bachmanii* (Kirtland)  
*Vanessa cardui* (L.)  
*Junonia coenia* (Hbn.)  
*Euptoieta claudia* (Cram.)  
*Danaus plexippus* (L.)

Most of these species overwinter in the SE coastal plain where they are multivoltine. As their populations expand during the summer, they move N and W, often penetrating into the Appalachians. Although they may reproduce during summer and fall, they generally cannot survive winter in NE Tennessee. There are exceptions, as evidenced by an April record for *Pyrgus communis*. In NE Tennessee, migrants are most likely to be found from mid-August through October. During this period *Atalopedes campestris* is one of the most common butterflies in gardens and disturbed areas. At the other extreme, *Papilio cresphontes*, *Pontia protodice*, and *Hylephila phyleus* are known from only one or two records. Remaining species are usually present every year in varying numbers. *Libytheana bachmanii* differs from the usual migrant pattern of occurrence in that it has been found from mid-June through mid-August. It is regularly present, but usually only as one or two individuals at a given time and place. We include it as a migrant because we have never collected overwintered individuals in spring.

We are not certain of the status of *Thymelicus lineola* (Ochs.) in NE Tennessee. It has been taken only once, near a campground in Sullivan Co. adjacent to a N-S interstate highway. This European species has spread rapidly southward since it was accidentally introduced into Canada around 1910 (Scott 1986), and there are records from SE Kentucky and SW Virginia (Opler 1983). If not already a resident, it is likely to become one soon.

While walking in the late 50's or early 60's, the senior author saw a single *Anaea andria* flying in a clover field in Sullivan Co. Without a net he could not capture it, but followed it for a distance and was certain of the identification. This species is resident around Center Hill

Lake, 130 km E of Nashville, and the junior author recently captured several overwintered individuals in Lee Co., SW Virginia. While we have not seen *A. andria* in NE Tennessee during the past 10 years, it is somewhat migratory (Scott 1986), and should be expected on occasion.

Southwest Virginia and N Georgia have more species than NE Tennessee, 120 and 108, respectively. This disparity is at least partly due to the fact that Virginia and Georgia have been collected longer than NE Tennessee.

*Amblyscirtes aesculapius* was the only species found in NE Tennessee that has not been recorded from SW Virginia. The Clarks (1951) recorded it only from the coastal plain of Virginia, but there are records from E Kentucky, and it probably occurs locally along rivers in SW Virginia. *Euchloe olympia* and *Clossiana bellona toddi* are resident in NE Tennessee, but are not known to occur in N Georgia. These species are at or near the limits of their ranges in NE Tennessee.

The 39 species recorded from SW Virginia and/or N Georgia not collected in NE Tennessee are listed in Table 2. Sixteen of these species are known only from SW Virginia, nine from N Georgia only, and fourteen occur in both regions.

Many species recorded from SW Virginia but not from NE Tennessee are northern species whose ranges extend southward in the Appalachian region. Southwest Virginia includes the entire breadth of the mountainous Blue Ridge Province, and elevations in the Valley and Ridge Province exceed 1200 m in places (Fenneman 1938). More extensive areas of high elevation coupled with higher latitude make SW Virginia more hospitable for some northern species than NE Tennessee.

Species recorded from N Georgia but not NE Tennessee include *Satyrrium kingi* (Klots & Clench), *Amblyscirtes carolina* (Skin.), *Agraulis vanillae* (L.), and other species more typical of the lowland Piedmont and Coastal Plain provinces. Relative to NE Tennessee, the Appalachian region of N Georgia is lower in elevation and has a milder climate. In particular, the prominent ridges that characterize the Ridge and Valley further N are absent (Fenneman 1938). Broad valleys open onto the Piedmont, while the oak-pine forest association and red-yellow podzolic soils characteristic of the Piedmont extend into the Georgia portion of the Ridge and Valley (Braun 1950, Walker 1969). These climatic and topographic factors create favorable habitats for some lowland species, and provide easy access for migrants.

We predict that the following species in SW Virginia and N Georgia will eventually be found resident in NE Tennessee:

*Thorybes confusus* Bell  
*Erynnis martialis* (Scudder)  
*Hesperia metea* (Scudder)

*Wallengrenia otho* (J. E. Smith)  
*Atrytonopsis hianna* (Scudder)  
*Satyrrium edwardsii* (G. & R.)

TABLE 2. Butterfly species occurring in SW Virginia (VA) and N Georgia (GA) but not recorded from NE Tennessee.

Species	State
<i>Thorybes confusus</i>	VA, GA
<i>Erynnis martialis</i>	VA, GA
<i>E. zarucco</i>	VA, GA
<i>E. lucilius</i>	VA
<i>E. persius</i>	VA
<i>Pyrgus centaurae</i>	VA
<i>Lerema accius</i>	VA, GA
<i>Hesperia metea</i>	VA, GA
<i>H. leonardus</i>	VA
<i>H. sassacus</i>	VA
<i>Polites mystic</i>	VA
<i>P. vibex</i>	VA
<i>Wallengrenia otho</i>	VA, GA
<i>Atrytone arogos</i>	VA
<i>Euphyes conspicua</i>	VA
<i>E. bimacula</i>	VA
<i>Atrytonopsis hianna</i>	VA, GA
<i>Panoquina ocola</i>	VA, GA
<i>Amblyscirtes carolina</i>	GA
<i>A. alternata</i>	GA
<i>Megathymus yuccae</i>	GA
<i>M. harrisi</i>	GA
<i>Zerene caesonia</i>	GA
<i>Eurema daira</i>	VA, GA
<i>Atlides halesus</i>	VA
<i>Satyrium edwardsii</i>	VA, GA
<i>S. kingi</i>	GA
<i>Incisalia irus</i>	VA, GA
<i>Fixenia ontario</i>	VA
<i>Calephelis borealis</i>	VA
<i>Agraulis vanillae</i>	GA
<i>Charidryas gorgone</i>	GA
<i>Speyeria idalia</i>	VA
<i>Clossiana selene</i>	VA
<i>Phyciodes batesii</i>	VA, GA
<i>Polygonia progne</i>	VA
<i>P. faunus</i>	VA, GA
<i>Enodia portlandia</i>	GA
<i>Satyrodes appalachia</i>	VA, GA

*Incisalia irus* (Godt.)  
*Phyciodes batesii* (Reak.)

*Polygonia faunus* (F.)  
*Satyrodes appalachia* (R. Chermock)

*Hesperia leonardus* (Harr.), *H. sassacus* (Harr.), *Speyeria idalia* (Drury), and *Polygonia progne* (Cram.) have been recorded from bordering counties in Virginia and North Carolina (Opler 1983) and also seem likely to be found in NE Tennessee eventually.

It is possible that *Amblyscirtes celia belli* H. A. Freeman occurs in NE Tennessee. We have taken it flying with *Wallengrenia otho* in

moist woods beside an arm of Loudon Reservoir near Knoxville, Tennessee, about 65 air km SW of our study area boundary. Similar habitats should occur around reservoirs in NE Tennessee.

Additional migratory species such as *Erynnis zarucco* (Luc.) and *Panoquina ocola* (Edw.) may eventually turn up also, but lack of direct access from the Piedmont is a hindrance to the movement of such species; to enter NE Tennessee, they must first pass through the rugged North Carolina portion of the Blue Ridge, or travel a considerable distance up valleys from Georgia.

Concentration of collecting efforts on species listed above should increase the number of butterfly species known from NE Tennessee to between 100 and 110.

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## GENERAL NOTE

### GLASSBERG, LEHMAN, AND PELLMYR COLLECTIONS TO THE SMITHSONIAN INSTITUTION

Dr. Jeffrey S. Glassberg has donated his collection of New World butterflies to the National Museum of Natural History (Smithsonian Institution). It consists of more than 2000 specimens, primarily Neotropical Theclinae (approximately 350 species). Dr. Glassberg is a molecular geneticist who lives in Chappaqua, New York, and is Vice President for Research of Lifecodes Corp. He has a strong interest in conservation and butterfly watching, and is currently President of the Xerces Society.

The Smithsonian Institution has received Mr. Robert Lehman's collection of Honduran Lepidoptera. There are 4222 meticulously spread specimens representing 1852 species, plus about 5000 papered specimens. The Macrolepidoptera are well represented, and there are many Pyralidae, Tortricidae, and Oecophoridae. Most of the specimens were collected along the wet Atlantic coast of Honduras, an area that is poorly represented in collections, and which augments the Smithsonian's strong holdings from Mexico, Guatemala, Costa Rica, and Panama. Mr. Lehman has been teaching elementary school science and, more recently, computer science, at the Mazapan School in La Ceiba, Honduras, for 9 years, and has been collecting in Honduras since 1968.

Dr. Olle Pellmyr has donated his collection of Fennoscandian (primarily Swedish) Lepidoptera to the Smithsonian Institution. It includes 6907 specimens of approximately 1200 species, and is rich in both Macro- and Microlepidoptera. Because so many Swedish species are close relatives of North American ones, this collection provides important comparative material. Dr. Pellmyr is an evolutionary biologist who works on chemical and ecological aspects of plant-pollinator mutualism and lepidopteran courtship behavior. He is a Swedish national, and currently a research scientist at the State University of New York at Stony Brook.

None of the collections contains primary type specimens.

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## BODY WEIGHT AND WING LENGTH CHANGES IN MINNESOTA POPULATIONS OF THE MONARCH BUTTERFLY

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**ABSTRACT.** Body weights and rear wing lengths were obtained from about 1900 monarch butterflies captured near Minneapolis, Minnesota, during the past decade. Mean values for both were lowest in immigrants and highest in subsequent generations. Mean wing length was highest in males. Mean body weights of immigrant females were higher than those of males, but mean male body weights were higher than those of females in subsequent generations. The data argue against the return to Minnesota of emigrants from the previous year, and suggest that attainment of large adult size could be one reason for monarch migration to northern regions.

**Additional key words:** Nymphalidae, *Danaus plexippus*, migration, sexual differences.

During the past several years workers in my laboratory have examined various aspects of the biology of the monarch butterfly, *Danaus plexippus* L. Our studies have impressed us with the great variation exhibited by monarch populations in our locality with respect to reproductive status, hormone titers, behavior, and other variables (Herman 1985). Monarch butterflies of both sexes also exhibit predictable changes in body weights and wing lengths during their residence in our area, and such changes are the topic of this report.

### MATERIALS AND METHODS

Animals used for this study were captured near Minneapolis, Minnesota, between 1976 and 1986. They were taken to the laboratory for measurement soon after capture, usually within a few h. Whole-body wet weights were determined to the nearest 1 mg using an analytical balance, and rear wing maximal lengths were measured to the nearest 0.5 mm with a ruler. Immigrant butterflies rarely arrive in our locality before 15 May, and most local monarchs emigrate by late September. The results are therefore for animals captured 16 May to 15 September, and data in Fig. 1 are summarized for 2-wk and 2-mo intervals during that period. All data are presented as mean  $\pm$  standard error; statistical analysis was done using Student's *t*-test.

### RESULTS

Mean wing lengths for both sexes were smallest during the 2-mo period 16 May-15 July (Fig. 1). Most of these animals were presumably immigrants from southern regions, since large numbers of monarchs

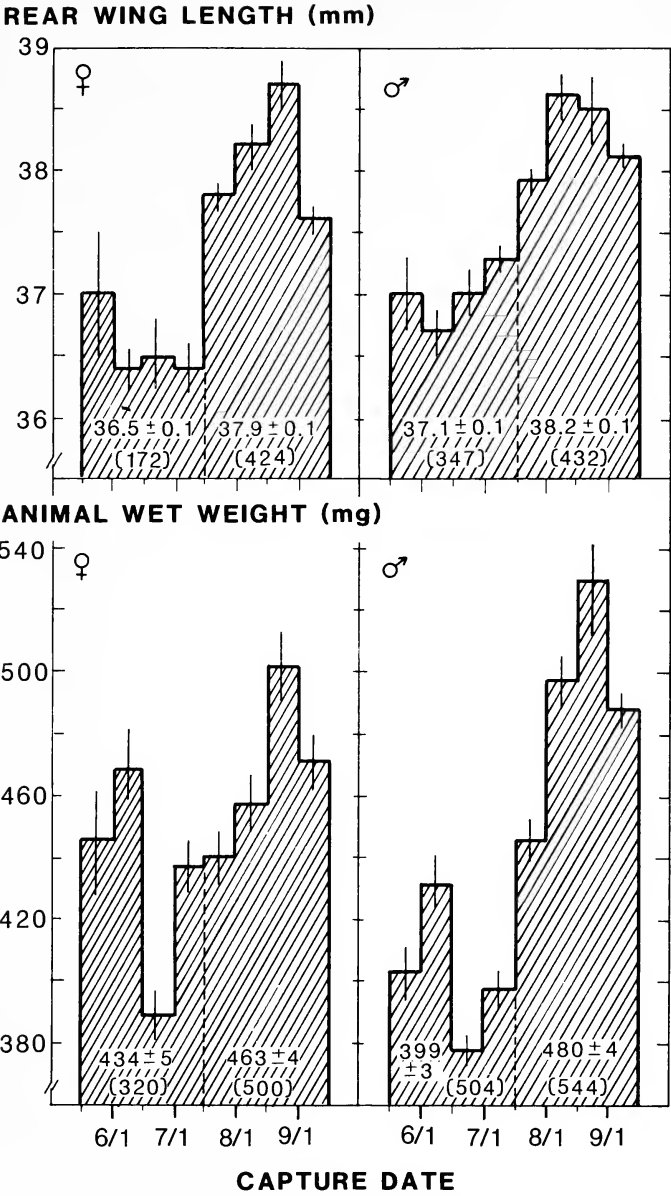


FIG. 1. Wing lengths and body weights of monarch butterflies captured near Minneapolis, Minnesota, 16 May–15 September. Data are summarized for 2-wk and 2-mo periods. Means for 2-mo periods are shown numerically, and number of individuals given in parentheses. Vertical lines indicate SE.

do not typically emerge in our area until early July. Mean wing length in both sexes increased significantly ( $P = 0.001$  for both sexes) in the 2nd 2-mo period 16 July–15 September. Presumably, most of the latter animals emerged in our locality. Mean female wing length increased 3.8% in the second 2-mo period, that of males, 3.0%. Mean male wing lengths were significantly larger than those of females in both the 1st ( $P = 0.001$ ) and 2nd ( $P = 0.05$ ) 2-mo periods. Mean wing lengths recorded 16 July–15 September were indistinguishable from those observed at emergence in monarchs reared on milkweed, *Asclepias syriaca* L., in our area in July and August:  $37.8 \pm 0.1$  mm ( $n = 100$ ) and  $38.0 \pm 0.1$  mm ( $n = 83$ ) for females and males, respectively, on the day of eclosion. Rear wing length varied from 29.5 to 42.0 mm in this study, and both extremes were observed in males.

Body weights of both sexes changed in a manner similar to that of wing lengths, with low mean values characterizing the mainly immigrant populations of 16 May–15 July, and significantly higher mean values observed in monarchs that had presumably emerged in our area 16 July–15 September (Fig. 1). Mean body weights for females were elevated 6.7% in the 2nd 2-mo period, those of males, 20.3%. Mean female body weights were significantly larger ( $P = 0.001$ ) than those of males 16 May–15 July, principally due to higher female weights of 16 May through 15 June. Male values were significantly higher ( $P = 0.005$ ) than those of females during the final 2-mo period. The lowest mean values for both sexes were recorded in late June, when senescence and death of immigrants is most pronounced, and the highest were recorded in late August, when reproduction generally ceases in our area. The increasing mean weights for both sexes from 1 July to 15 August were recorded for populations consisting principally of actively reproducing monarchs of various ages. Mean body weights of wild-caught butterflies never reached the mean values ( $680 \pm 32$  mg [ $n = 26$ ] and  $652 \pm 11$  mg [ $n = 109$ ], respectively) measured on day of eclosion for females and males reared in our area. Body weights ranged from 195 to 836 mg during this study, and both extremes were again found in males.

#### DISCUSSION

The data show that predictable variations occur in rear wing lengths and body weights during the period that monarch butterflies reside near Minneapolis. Small wings and low weights characterize the immigrant population, and both parameters increase significantly in both sexes when monarchs that have apparently emerged in our area predominate in the local population, as they normally do after 1 July. Causes of these variations, and their possible adaptive value, are un-

determined. However, the data suggest that local environmental factors (nutrient value of foodplant, temperature, or photoperiod) during June, July and August may provide optimal conditions for larval growth, and thereby result in larger adults with longer wings. If so, suboptimal conditions for larval development of the presumed immigrant generation in southern areas could account for reduced size in immigrant butterflies. This line of reasoning implies that northward migration in spring could be, to at least some extent, an adaptation for locating regions that optimize adult size. Larger adults may have a greater probability of successful southward migration, survival in the overwintering colonies, or remigration.

The smaller wings of immigrants might somehow facilitate northward migration, while the larger wings of animals emerging in late August and September may be more advantageous for southward migratory flights. Perhaps larger wings are more efficient for soaring and gliding, phenomena reported only for monarchs migrating south (Gibo 1981). Immigrant males with smaller wings might also be more successful at mating, as reported for males in Mexican overwintering colonies (Van Hook 1986). James (1984) noted no significant differences in wing lengths of Australian monarchs observed during a full year.

The data on monarch body weight generally agree with those in other reports (Cenedella 1971, Brown & Chippendale 1974, Brower & Glazier 1975). Other studies have reported significantly higher body weights of males in southward migrating and overwintering monarch populations (Tuskes & Brower 1978, Chaplin & Wells 1982). However, others have apparently not observed periods in the monarch annual cycle when females are significantly heavier than males, as Fig. 1 records for immigrants to our area.

Data in Fig. 1 argue against the return to our locality of monarchs that emigrated the previous year. Our immigrants, especially females, have intermediate weights, and, based on body weight and external appearance, most appear to be young or middle-aged, certainly not old. Immigrants to our area also exhibit both senescence and precipitous weight loss (Fig. 1) within 2–4 wk after arrival, and it seems reasonable to assume that comparable rates of aging and weight loss occur after monarchs leave Mexican overwintering colonies. In view of these observations, it is unlikely that overwintering monarchs could leave Mexican colonies in mid-March (Norman 1986), fly northward for 8–10 wk while actively breeding, and arrive in our area with body weight and external appearance comparable to young populations of July. Similarly, smaller wings of our immigrants suggest they are not members of the emigrant generation of the previous year, since emigrants have significantly larger wings. In addition, monarchs captured in Mexican col-



onies in February and March 1984 had wings comparable in length to our emigrants, and significantly larger than those of our immigrants (Herman unpubl.). For these reasons, the data support an earlier conclusion (Herman 1985), and that of Malcolm et al. (1986), that most immigrants to the northern United States are probably one generation removed from individuals forming Mexican overwintering colonies.

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## HABITAT AND RANGE OF *EUPHYDRYAS GILLETTII* (NYMPHALIDAE)

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**ABSTRACT.** Fifteen sites occupied by *Euphydryas gillettii* are compared according to 10 characteristics. All sites are moist, open, mostly montane meadows, many with a history of disturbance, commonly fire. Population size correlates with relative availability of nectar but not with overall abundance of the usual hostplant, *Lonicera involucrata*. Habitats at higher latitudes often have a southerly exposure. Reduction in hostplant size at higher latitudes contributes to the northern range limit. Three populations likely have become extinct since 1960, but the species range does not appear to be changing.

**Additional key words:** nectar, *Lonicera involucrata*, biogeography, extinction.

*Euphydryas gillettii* (Barnes), a checkerspot butterfly, occurs in discrete, isolated populations (Williams et al. 1984) in the central and northern Rocky Mountains (Ferris & Brown 1981). It is attractive and easily caught but uncommon and not often collected. Though usually considered a montane species (Williams et al. 1984), variation in sites occupied by *E. gillettii* has not been studied, and lack of knowledge about its habitats has led to uncertainty about its range.

Here I report characteristics of sites occupied by *E. gillettii*, present range of the species, and factors influencing its distributional pattern. This study is based on direct observation of the habitats of 15 populations throughout the range, thus affording an uncommon view of habitat variability in a single insect species.

### METHODS

Populations of *E. gillettii* were located through correspondence with collectors and researchers listed in Acknowledgments, examination of specimen labels in collections listed in Acknowledgments, and a survey of published reports (*News Lepid. Soc.*, Seasonal Summaries 1960-1986). When directions were sufficient to pinpoint locations on a topographic map, I visited the sites, and assessed relative population size and habitat characteristics.

Population size was determined by a one-day count of adults, egg masses, and larval webs. Egg masses of *E. gillettii* are distinctive, easily found, and readily counted, thus permitting quantitative comparisons of colony size even after the flight season; in fact, egg mass counts are better indicators of population size than adult counts because the former are independent of weather. Eggs do not begin hatching until late in the flight season (Williams et al. 1984), so developmental state of egg masses at each site indicated timing of the count relative to flight season.

Females average one to two egg masses per individual (unpubl.); thus, relative population size can be estimated from sum of egg masses and adults.

In addition to population size, I recorded nine site characteristics, and searched for evidence of disturbance. Observations were quantified as much as possible for later analysis. Each site is marked on U.S. Geological Survey and Canada Department of Energy, Mines & Resources topographic maps in my possession, and latitude and elevation were measured directly from these maps. I used a compass as well as contour lines on the maps to determine exposure. I recorded number of distinct shrubs or clumps of the usual hostplant, *Lonicera involucrata* (Rich.) Banks (Caprifoliaceae) (Comstock 1940, Williams et al. 1984), in open areas where egg masses and adults were found. Nectar sources were identified (Hitchcock & Cronquist 1973), and relative nectar availability was determined by site comparison. Nearby trees were identified and cored with a 5 mm diam increment borer for age determination. Presence and distance to standing water and streams were recorded. I inferred source and history of disturbance from characteristics such as tree species and age, charring, stems gnawed by beavers, and location in a flood plain.

## RESULTS

### Populations

I visited 29 localities reported as sites for *Euphydryas gillettii* and found populations at 13. With my 2 previous study sites (Williams et al. 1984), I had a total of 15 colonies throughout the geographic distribution of the species for comparison. More than 15 egg masses and adults were found at 7 sites ("large" populations), while fewer than 15 were found at 8 sites ("small" populations) (Table 1).

### Habitat Characteristics

All occupied sites are wet (Table 1). Most have a small stream passing through, though several are marshy without obvious flowing water; *E. gillettii* occurs infrequently near rivers, perhaps because of flood disturbance to hostplants, nectar sources, larvae, and adults. In habitat characteristics, *E. gillettii* is similar to its congener *E. phaeton* (Drury) (Scudder 1889). There is no observable relation between population size and type of water present.

There appears to be a correlation between colony size and nectar abundance ( $\chi^2 = 3.2$ ,  $df = 1$ ,  $P = 0.07$ ). Only two sites have large populations with low nectar availability, but these populations are marginally "large" (sites 7 & 9, Table 1). Total amount of nectar is also important in *Euphydryas editha* (Boisduval), influencing its population

TABLE 1. Characteristics of 15 sites occupied by *Euphydryas gillettii*.

Site no.	Colony size <sup>1</sup>	<i>Lonticera invol.</i> abundance <sup>2</sup>	Nectar availability	Nearby trees (age of largest to nearest 5 yr)	Water (stream width)	Disturbance
1	>30	>30	High	Lodgepole pine (75) Engelmann spruce (65)	Stream (<1 m)	Fire <sup>3</sup>
2	>30	>30	High	Quaking aspen (60) Subalpine fir (75)	Streams (<1 m)	None; meadow edge
3	7	10	Low	Engelmann spruce (150)	Stream (1–3 m)	None; meadow edge
4	2	10	Low	Lodgepole pine (55)	Marshy	Fire; wet soil
5	4	20	Low	Lodgepole pine (90) Quaking aspen (65)	Stream (<1 m)	Fire; logging
6	>30	20	High	Subalpine fir (155) Lodgepole pine (15)	Streams (<1 m)	Fire <sup>3</sup> ; logging
7	18	10	Low	Cottonwood (40) Lodgepole pine	Stream (1–3 m)	Beaver activity
8	21	10	High	Lodgepole pine (65)	Stream (>5 m)	Flooding
9	22	20	Low	Lodgepole pine (95) Engelmann spruce (70)	Marshy, stream (<1 m)	Wet soil
10	8	>30	High	Lodgepole pine (55) Engelmann spruce (50) Subalpine fir (40)	Stream (<1 m)	Fire?; meadow edge
11	7	5	Low	Subalpine fir (95) Engelmann spruce	Marshy	Fire <sup>3</sup>
12	3	>30	Low	Lodgepole pine	Stream (1–3 m)	Flooding; fire?
13	1	20	Low	Engelmann spruce (195) Lodgepole pine (40)	Stream (1–3 m)	Fire <sup>3</sup>
14	2	20	Low	Willow (no trees)	Marshy, stream (<1 m)	Wet soil; grazing
15	>30	5	High	Lodgepole pine (75)	Marshy	None; meadow edge

<sup>1</sup> Total number eggs and adults.  
<sup>2</sup> Approximate number *Lonticera* clumps in 30 × 30 m quadrat.  
<sup>3</sup> Charred tree trunks.

dynamics (Murphy et al. 1983). Nectar is supplied by a number of genera (Table 2), mostly commonly *Aster*, *Senecio*, and *Agoseris*, but each occurs conspicuously at no more than 9 of the 15 sites. Williams et al. (1984) found the butterflies to switch nectar sources readily when an early source senesces. Total amount of nectar thus appears more important than particular sources.

Hostplants were considered highly abundant when there were more than 15 distinct shrubs or clumps. In contrast to nectar availability, hostplant abundance does not correlate directly with population size ( $\chi^2 = 0.1$ ,  $df = 1$ ,  $P > 0.5$ ). Reasons are considered later.

Most sites have been disturbed (Table 1), with fire being the commonest natural source. Lodgepole pine, *Pinus contorta* Dougl., is com-

TABLE 2. Common nectar sources for *Euphydryas gillettii* at 15 study sites.

Genus	Number of sites where present	Genus	Number of sites where present
<i>Aster</i>	9	<i>Polygonum</i>	2
<i>Senecio</i>	8	<i>Antennaria</i>	1
<i>Agoseris</i>	7	<i>Chrysanthemum</i>	1
<i>Geranium</i>	6	<i>Cirsium</i>	1
<i>Achillea</i>	5	<i>Geum</i>	1
<i>Heracleum</i>	5	<i>Helianthella</i>	1
<i>Potentilla</i>	4	<i>Saxifraga</i>	1
<i>Valeriana</i>	3	<i>Solidago</i>	1

mon near colonies (Table 1), indicating common disturbance history in these areas (Pfister et al. 1977). Whatever the cause, disturbance opens a site for growth by more hostplants and nectar sources. The few sites not clearly showing disturbance are on edges of permanent wet meadows of grasses and sedges.

At higher latitudes, occupied sites occur at lower elevations (Fig. 1,  $r^2 = 0.49$ ,  $P < 0.005$ ). This result likely reflects colder climates and reduced height of mountains at higher latitudes. Furthermore, importance of a minimum growing season length is shown in frequent southerly exposure of sites at higher latitudes, in contrast to the variable exposure of sites at lower latitudes (Fig. 1). All large northern populations occupy sites with southern exposure, while southern sites show no observable relation between population size and exposure. Williams (1981) demonstrated the importance of within-habitat exposure effects; current results suggest larger-scale influences as well.

### Range

Available records of *E. gillettii* are mapped in Fig. 2. Sightings are concentrated in the mountainous regions of W Wyoming, central Idaho, NW Montana, and SW Alberta. Some regions for which there are only older records, such as Yellowstone National Park and SW Montana, undoubtedly support populations, but their inaccessibility makes collecting sporadic. Continued existence of *E. gillettii* in extreme SW Wyoming is questionable because extensive search has failed to uncover specimens (C. F. Gillette pers. comm.). A reported record from central Montana may be erroneous. There is also a single museum specimen from Ontario, but improbable date as well as location suggest mislabeling.

Sites in Alberta have smaller populations of butterflies than do those farther south, and all northern sites have one characteristic in common: *Lonicera involucrata* does not reach the large size and luxuriant growth characteristic of Wyoming and Montana sites. In moist areas at higher



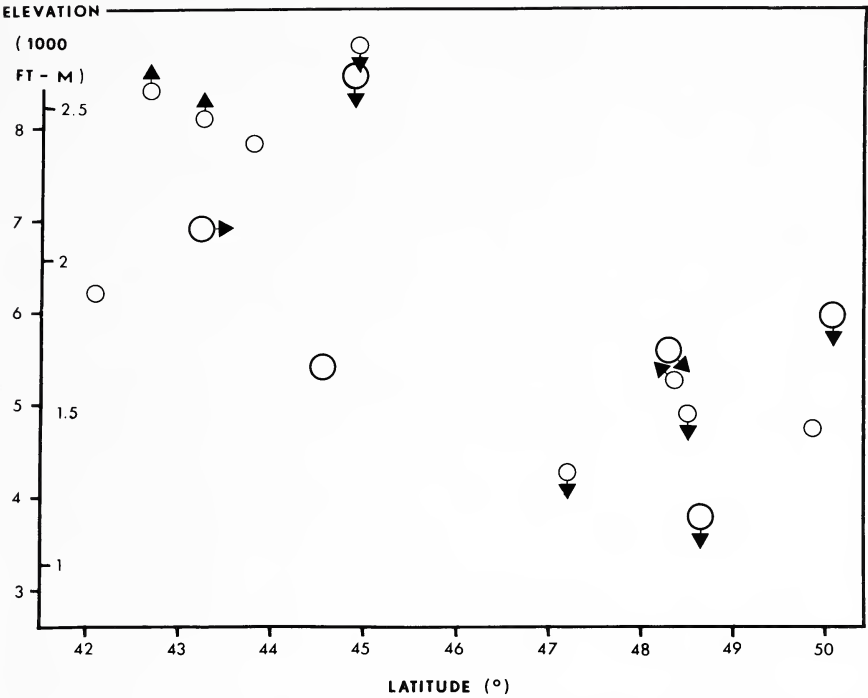


FIG. 1. Elevation and latitude of fifteen *Euphydryas gillettii* sites. Large circles represent "large" populations. Arrows pointing down indicate sites with southerly exposure; those pointing right, easterly exposure; etc. Absence of arrow indicates site has no obvious slope.

latitudes, willows (*Salix* spp.) are often taller than *L. involucrata*, shading them and making them less accessible to searching females; this rarely occurs at lower latitudes. Oviposition sites are therefore scarcer than at lower latitudes, because oviposition occurs on the highest leaves of hostplants that are fully exposed to sunlight (Williams 1981, Williams et al. 1984).

DISCUSSION

There appear to be four reasons for lack of correlation between population size and abundance of *L. involucrata*. First, and most importantly, this plant grows in moist areas regardless of amount of sunlight, while the butterfly requires sunlit hostplants (Williams 1981). In fact, the most luxuriant hostplants often grow in shade of conifers, but are not used as oviposition sites. Second, an extension of the first, much *L. involucrata* is over-shaded by willows at high latitudes, thus providing fewer potential oviposition sites in such areas. Third, some *Euphy-*

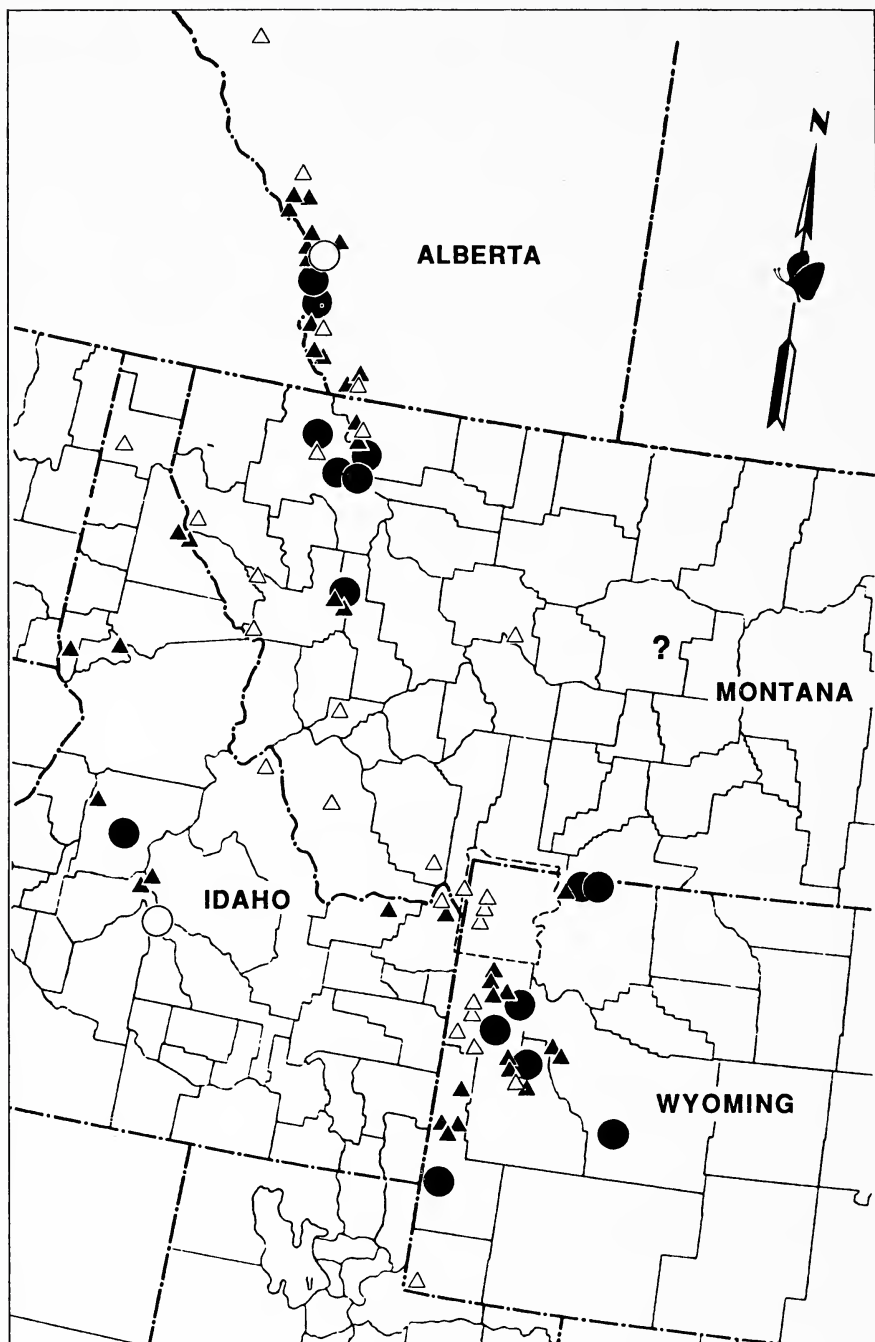


FIG. 2. Range of *Euphydryas gillettii*. Closed circles are sites described in this study; open circles are locations of populations believed extinct; closed triangles are locations

*dryas gillettii* populations are mostly biennial (Williams et al. 1984), and so may fluctuate greatly in abundance from year to year. While most *E. gillettii* sites are characterized by abundant *Lonicera involucrata*, these three factors limit the size of an observed butterfly population to less than might be expected given the total amount of *Lonicera*. The fourth reason is butterfly use of alternative hostplants.

Only at one site was the colony larger than would seem possible given the amount of nearby *L. involucrata*. That population (site 15, Table 1) lives where *L. involucrata* is uncommon, and the butterflies oviposit extensively on two other plants, *Pedicularis* and another *Lonicera* (in prep.). There are several possible reasons for dietary expansion in butterflies (Singer 1971, 1983); but whatever they may be for this population, other study populations have not followed suit, even though all known alternative hostplants grow throughout the *Euphydryas gillettii* range. Except for site 1, where an alternative hostplant was chosen at low frequency (less than 4% of egg masses, Williams & Bowers 1987), I did not find eggs on or see ovipositional behavior near other plants at the other 14 sites. Because of the known use of alternative hostplants, I expect other *E. gillettii* populations use alternative hostplants as well. The relation between population size and *Lonicera involucrata* abundance is thus weaker than has been widely accepted.

Because its hostplants and nectar sources require wet sites, and because adults and larvae require sunlit areas for warmth, *Euphydryas gillettii* most often occurs in open montane meadows. The one study population that is not montane occupies a permanently wet, grazed seepage area in the transition zone. Several populations were observed along forested edges of seemingly permanent montane meadows; such meadows may change little through time because of allelopathic interactions of meadow vegetation or soil instability. More commonly, open sites are created temporarily through disturbance. The most frequent disturbance is fire, and most study sites have clearly been affected by it. Other forms of disturbance, such as flooding, beaver activity, or human activities like grazing and logging, also serve to open forested areas.

Vegetational succession in disturbed areas leads to changes that make sites less suitable through time. In particular, encroachment by surrounding forest leads to greater evapotranspiration, producing a drier site and thereby limiting growth of hostplants and nectar sources. Furthermore, invasion by trees reduces the sunlight that reaches the shrub

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where *E. gillettii* has been seen since 1960; open triangles are records before 1960; question mark denotes uncertain record.

and herb layer, thus eliminating warmer microsites preferred for oviposition (Williams 1981).

Life in disturbed sites suggests that *E. gillettii* populations are subject to periodic extinction like *E. editha* (Singer & Ehrlich 1979), and such appears to be the case. I identified with precision one site where *E. gillettii* was collected in the 1960's, but by 1983 vegetational succession had taken place, most remaining *Lonicera involucrata* was shaded, and no sign of butterflies could be found. Furthermore, human development of recreational areas has led to loss of additional populations, one known and one suspected.

Habitat requirements of *E. gillettii*, including moisture for hostplants and nectar, and sunlight for larvae and ovipositing females, produce the limits of its geographic distribution. Thus, plains east of the Rockies and arid basins westward form effective biogeographic barriers to dispersal in either direction because of lack of water. Holdren and Ehrlich (1981) have shown that another arid region, the Red Desert of S Wyoming, is the southern barrier since they successfully transplanted individuals across the barrier to central Colorado where one colony has survived since 1977. Their transplant locales are similar to natural habitats farther north in being wet and having an abundance of nectar and *Lonicera involucrata*.

The northern range limit has been assumed to result from lower temperatures and shorter growing season. However, all the Alberta sites have much smaller *L. involucrata*, and willows dominate northern wet sites by growing taller than other shrubs. All populations of the butterfly at higher latitudes are smaller as well. Although no northern populations have been found to use hostplants other than *L. involucrata*, alternative hostplants used elsewhere also decline in abundance at higher latitudes. It seems likely that competition by willows reduces size and perhaps density of potential hostplants. Thus, fewer oviposition sites and poorer (more shaded) ones would be found during normal hostplant searching by females (Williams et al. 1984). I suggest that loss of oviposition sites contributes, along with shorter growing season, to the northern limit.

*Euphydryas gillettii* is uncommon, but there is no evidence that its range has been changing in recent decades. The greatest conservation advantage this species has compared to other uncommon species is that its habitat lies largely in mountainous areas that are not readily accessible and in which there is little immediate potential for human modification. Its greatest conservation disadvantage is its occurrence through a limited range in discrete, localized populations, which are individually susceptible to disturbance and extinction.

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## BIOLOGY OF *POLYGONIA PROGNE NIGROZEPHYRUS* AND RELATED TAXA (NYMPHALIDAE)

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**ABSTRACT.** The life history of *Polygonia progne nigrozephyrus* is compared with that of *P. gracilis zephyrus*, *P. faunus hylas*, and *P. satyrus* in Colorado. Adult predator deterrent behaviors occur: adults resemble leaves as they rest on twigs showing leaflike undersides, roost with forewings drawn forward with antennae resting between them, and feign death when handled. Larvae also have predator-avoidance strategies: scoli presumably act as a physical deterrence, small larvae can drop using a silk thread, a ventral neck gland possibly repels predators, larvae vomit on an attacker, older larvae resemble twigs as they rest in a three-dimensional twisted-S shape, pupae resemble a dried curled leaf or short twig. Larval host plants differ between species, with some overlap. Identification features for the four species are presented for each stage. Despite adult similarity of *P. progne nigrozephyrus* and *P. gracilis zephyrus*, *P. g. zephyrus* larvae most resemble those of *P. faunus*.

**Additional key words:** *Polygonia gracilis*, *P. faunus*, *P. satyrus*, predator deterrence, chaetotaxy.

Scott (1984) described *P. progne nigrozephyrus* which occurs in Colorado-S Wyoming-Utah-SE Idaho-NE Nevada. It resembles *P. gracilis zephyrus* (Edw.) on the upperside, *P. p. progne* (Cram.) on the underside and in male abdominal structure, and was long confused with *zephyrus*. *Polygonia p. nigrozephyrus* is certainly the same species as *oreas* (Edw.), but some may question whether it and *oreas* belong to *P. progne*. Early stages of *nigrozephyrus* are similar to those of *oreas* and *progne*, and are distinct from *zephyrus* and other *Polygonia*; wing undersides and abdominal structures resemble those of *progne*. Therefore, *nigrozephyrus* does seem to be a subspecies of *progne*.

Since 1984, minor differences between populations of *nigrozephyrus* in Colorado have been found. Adults from the E slope of the continental divide in the Front Range usually have the dorsal hindwing darker because the submarginal spots are the same size as those of *P. g. zephyrus*, whereas adults from the W slope usually have the spots larger like those of *P. satyrus* (Edw.). However, the difference is not great enough to warrant a new name for W slope populations, and some adults from each area resemble those from the other. The Front Range populations may have slightly darker dorsal hindwings because of occasional immigration of subspecies *progne*, which has a very dark dorsal hindwing margin.

An additional difference not mentioned by Scott (1984) between some *P. p. progne* adults and other *Polygonia*, first noticed by W. H. Edwards, involves one of the dark stripes in the ventral forewing discal cell: in most *P. p. progne* the anterior stripe is unbroken, whereas in some of

them and in other subspecies and species the stripe is broken into two parts.

For oviposition and larval rearing, cut host-plant sprigs were put into water-filled vials, cotton-plugged so the water would not drain when vials were on their sides. For older larvae, large host branches were cut and placed in wet sand.

### Adult Stage

Adults bask with wings spread (dorsal basking). In the laboratory, some *nigrozephyrus* females closed the wings above the thorax and vibrated them rapidly (up to 2 mm apart at the tips) when lights were turned on in the morning; this is shivering behavior to raise the thorax temperature prior to flight.

Adults of *nigrozephyrus*, *zephyrus*, and *faunus* (Edw.), as well as *Nymphalis milberti* (God.), roost on twigs with wings closed, forewings drawn far forward (nearly out of hindwings) and covering the head and antennae which rest between the forewings. This posture perfects the resemblance to a leaf on the twig by elongating the "leaf", breaking up its margin, and hiding antennae to avoid predation during fall, winter, and spring. Adults frequently feign death when handled, which would also signal a predator that the butterfly is a dead leaf.

There is evidently a circadian rhythm of oviposition, because females laid eggs in the laboratory only during daytime, and even when lights remained lit females began roosting in late afternoon. For obtaining oviposition, fluorescent bulbs were superior to incandescent bulbs, probably because the former produce a greater and more natural amount of ultraviolet light.

### Immature Stages

**Host plants.** *Polygonia progne nigrozephyrus* feeds on gooseberry: *Ribes inerme* Rydb., in Delta and Douglas counties, Colorado, *R. leptanthum* Gray at Williams Canyon, El Paso Co., Colorado. In the laboratory, *nigrozephyrus* larvae accepted leaves of *Ribes inerme*, but refused wax currant, *R. cereum* Dougl., and ate very little golden currant, *R. aureum* Pursh. They ate only leaves. Additional host records for *P. p. progne*, based on preserved larvae in the Smithsonian, are gooseberry (St. Albans, West Virginia, Monticello, New York) and currant (Centreville, Rhode Island).

*Polygonia gracilis zephyrus* usually eats *Ribes cereum* in Colorado. However, I found an egg on *R. inerme* at Tinytown, Jefferson Co., on 2 June 1984, and reared it to a mature larva; and a larva under a *R. inerme* leaf 5 km W Idledale, Jefferson Co., on 12 June 1984, which I reared to an adult. In the laboratory, *zephyrus* larvae eat *R. cereum*,

and do not move off its leaves to eat adjacent *R. inerme* leaves, although larvae will also accept *inerme*. Additional host plants of *zephyrus* are *Ribes sanguineum* (Jones 1951), and *Rhododendron occidentale* (larvae reared to adults, Big Trees Park, Calaveras Co., California, 4 June 1983, J. F. Emmel & S. O. Mattoon).

*Polygonia faunus hylas* (Edw.) usually eats *Salix*, but I found three first-stage larvae and five eggshells under leaves of *Ribes inerme* at Tinytown on 26 May 1984, and an adult emerged 20 June. In the laboratory, *faunus* larvae refused *Ribes aureum* leaves, but ate *R. inerme* and preferred it to *R. cereum*.

Thus all three *Polygonia* will eat *Ribes inerme* occasionally.

The only known Colorado host of *P. satyrus* is *Urtica dioica gracilis* (Ait.) Sel., though *Humulus lupulus* L. is eaten elsewhere. In the laboratory, *satyrus* larvae accepted *Humulus* and *Urtica* leaves equally well.

### Life Cycle

Five larval instars have the following approximate head widths, respectively: 0.4, 0.7, 1.2, 1.7, 2.6 mm. Stage 1 is easily recognized by its black head without scoli; stage 2 has head scoli but is still black; stage 3 has head scoli but is black usually with an ochre pattern tending toward the pattern of stages 4–5. Usual laboratory durations of *nigrozephyrus* stages at 19°C were: egg, 5–6 days; larval stages, 3, 2.5, 2, 2, 4 days, respectively; and pupa, 9–10 days; totalling 27–30 days. In the cooler and more variable temperatures of nature, these periods are probably nearly doubled, so that adults should appear by late July–early August, although eggs laid in late April might produce the few fresh late-June adults known in nature. A *faunus* stage 1 larva found 26 May emerged as an adult 20 June in the laboratory, even though *faunus* emerges in nature only in late July and August. The laboratory life cycle of *P. p. progne* is 31–32 days (Edwards 1880), of *P. interrogationis* 28–40 days (Edwards 1882b), and of *P. comma* 27–33 days (Edwards 1882a). Thus all *Polygonia* have similar developmental rates indoors, and all have five larval stages. However, in Colorado *P. faunus* and *P. progne nigrozephyrus* have only one generation per year, while *P. satyrus* and *P. gracilis zephyrus* have two generations at low altitude and one at high altitude; and *P. interrogationis* has two or three generations.

### Predator-Avoidance Structures and Behavior

Stinkbugs and ants were found on *R. inerme* host plants and may prey on immatures.

The scoli of stage 2–5 larvae presumably physically deter predators.

They slightly hurt the human skin when touched, evidently a physical puncturing rather than an urticating chemical.

A ventral neck gland occurs on stage 2–5 larvae of all 4 *Polygonia* species; it contains 2 internal transverse dark secretory pads which perhaps produce repellent chemicals.

When grasped, the larva often bends its head around and vomits green fluid onto the attacker.

Fourth- and fifth-stage larvae of *nigrozephyrus* grasp a twig with the prolegs, bend the front part of the body right or left, and raise the end of the abdomen. This “corkscrew” posture may make the larva resemble a dead leaf or twisted twig, perhaps lessening predation by birds. This posture also occurs in ssp. *progne* (Edwards 1880) and in *satyrus* (C. F. Gillette pers. comm.).

Young larvae of all four species rest on the underside of a leaf, and when older may also rest on a twig. Only older larvae of *P. satyrus*, also *P. comma*, live in a nest. It is made by chewing the base of the leaf on each side, thus making it droop, and silking *Urtica* leaf edges down and together below the enclosed larva, which rests on the leaf underside.

Disturbed young larvae can extrude a silk thread as they fall, then crawl up the thread to return to the plant.

Pupae are constricted in the middle where silver spots also visually break up the outline, making the pupa resemble a dead, shriveled leaf or twig.

Gooseberry hosts are armed with sharp spines which act as physical protection against vertebrates. A punctured pupa recovered completely.

### Descriptions of Early Stages

Colors are based on live individuals. Immatures have been deposited in the Smithsonian Institution. Many dozen individuals of *Polygonia p. nigrozephyrus* were reared from eggs laid by females from NE of Cedaredge, Delta Co., and Nighthawk, Douglas Co. Each stage is described, and is followed by comparisons with the other three *Polygonia* species and subspecies, each of which were represented by less than 10 individuals. Segments are named T1 for prothorax, A3 for abdominal segment 3, etc. (Fig. 3). Scoli are named with the letter B followed by name of nearest primary seta. They are not preceded by S because of confusion with primary seta SD1, etc.; sp is spiracle; VNG is ventral neck gland on older larvae. Names of setae are from Hinton (1946) and Scott (1986), with slight modifications (Scott 1988) that improve homology and make head and body setal nomenclature different to avoid confusion.

**Egg.** Green, averaging 8.6 vertical ribs (Table 1), each rib steep-walled, increasing in height to maximum at top, then disappearing; 40–50 horizontal ribs forming ladder between adjacent vertical ribs; the day before hatching turning blackish with transparent silvery-reflecting shell as larva becomes partly visible.

**Comparison.** All *Polygonia* eggs green. *Polygonia p. progne* has 8–9 ribs, *P. g. zephyrus* averages 9.8, other *Polygonia* average 10.4–11.5 (Table 1).

**First-stage larva** (Figs. 1, 4, 5, 9, 11, 12, 16). Head black without pattern or horns. Body dark brown with long black setae, bumplike bases of which are chitin brown; with

TABLE 1. Number of vertical ribs on eggs.

Taxon	Mean	SD	Range	N	Source
<i>Polygonia p. nigrozephyrus</i>	8.6	0.55	8-10	40	this paper
<i>P. p. progne</i>	—	—	8-9	—	Edwards (1880)
<i>P. g. zephyrus</i>	9.8	0.59	9-11	27	this paper
<i>P. satyrus</i>	10.4	0.54	10-12	43	this paper
<i>P. faunus</i>	10.5	0.63	10-12	31	this paper
<i>P. interrogationis</i>	—	—	8-10	—	Edwards (1882b), Pyle (1981)
<i>P. comma</i> (Colo.)	11.5	0.50	11-12	58	this paper
<i>P. comma</i> (Minn.)	10.6	0.54	10-12	38	this paper
<i>Nymphalis vau-album</i> (D. & S.)	11.0	—	9-12	—	C. F. Gillette, pers. comm.

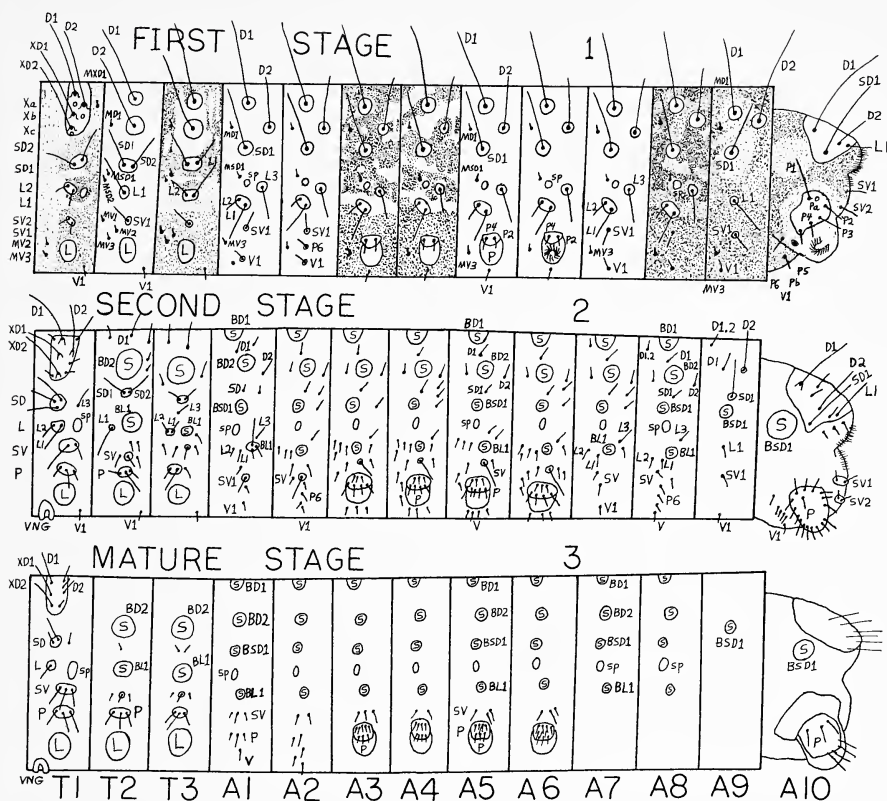
cream spots (Fig. 1) as follows: front half of T1 cream except for small supralateral brown patch on some larvae; T1 cream in front of, behind, just beside black prothoracic shield; rest of T1 brown except for 2 cream dashes extending rearward above, below spiracle. T2-3 brown, large yellow-cream patch around D2, smaller cream patch around L1-2. A2, A4, A6 brown, with 4 pale patches: broad cream mid-dorsal V aimed posteriorly on anterior part of each segment; broad yellow-cream patch below D1; narrow supralateral light brown dash; long cream sublateral dash. A1, A3, A5, A7 brown, with 4 light brown patches on each side corresponding to pale patches on A2, A4, A6; sublateral dash cream on A3, A5, A7, A8. A8 same as A7 but 3 upper patches slightly creamier. A9 brown, subdorsal cream patch twice as long vertically as horizontally. A10 brown, suranal plate black, proleg cream, proleg plate brown, large circular cream supralateral patch.

**Comparison.** Other *Polygonia* larvae very similar, with black hornless head and similar body pattern. *Polygonia satyrus* same as *nigrozephyrus*, pale bumps cream-white, a few creamy sublateral dashes. *Polygonia g. zephyrus* same as *nigrozephyrus*, except pale bumps cream-white instead of yellow-white, seta D1 on T3 on whiter bump as is seta D2, no supralateral brown patch on front of T1 though it appears on some second-stage larvae so may be individual trait, supralateral dash on A2, A4, A6 cream, A1, A3, A5, A7, A8 all brown except for lateral cream dash. *Polygonia interrogationis* similar (Edwards 1882b), but *P. comma* "whitish-green" (Edwards 1882a). *Polygonia faunus* larvae differ from all other *Polygonia* in having white areas expanded away from bumps: for instance, white patch on T2, T3 includes both D1, D2 setae; on A2, A4, A6 white V lengthened anteriorly, subdorsal white patches below D1 extend posteriorly.

**Second-stage larva** (Figs. 2, 6-8, 17). Head black with 2 short black spiny horns (BPA2 scoli) each with 1 long seta on tip, 5 setae on crown just below, no setae on long stalks; bases of PA1, AG3, LH1, O2 pale, membranous; very narrow short pale line along middorsal groove. Body reddish brown, brownish orange toward rear, similar to 1st stage in pattern, prothorax mostly orangish yellow; orange V's on top of A2, A4, A6, yellow-cream areas of first stage now orange, scoli present with bases orangish. Scoli BD2 on A2, A4, A6 ochre on some larvae, mostly brown on most, other scoli black. BD2 scoli on T2, T3, A2, A4, A6 rest on large orange bumps making segments conspicuously paler, other scoli rest on small orangish bumps. Body has weak cream mid-dorsal, subdorsal spots which help form abdominal V's; remaining segments have thin wavy lateral cream line between BL1 scoli, thin wavy supralateral cream line between BSD1 scoli. Tiny pale subdorsal transverse dashes present. Ventral neck gland present.

**Comparison.** *Polygonia g. zephyrus* has slightly shorter horns, body undergoes less color change from first stage: color pattern the same, pale patches still white, though BD2 on A2, A4, A6 yellow-cream, in some larvae blackish, making segments still paler on top, other scoli black. Only BD2 on T2-3, A2, A4, A6 rest on yellow-cream bumps; other scoli rest on small whitish bumps. Tiny cream transverse dashes occur behind, before BD2 on A2, A4, A6 to help form V's as in *P. satyrus*; middorsal, subdorsal, supralateral, lateral



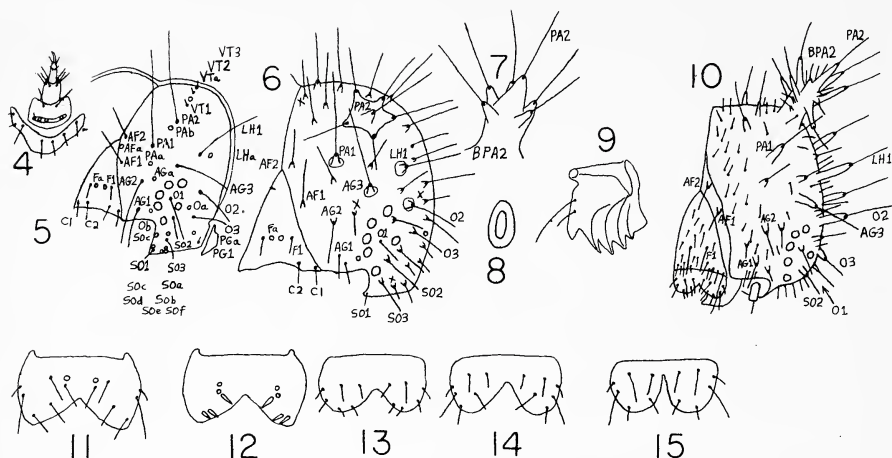


FIGS. 1–3. Setal maps of *Polygonia progne nigrozephyrus* larvae. 1, First stage. Color pattern shown on some segments, except that plates at base of setae, including prothoracic shield and suranal plate, are dark brown; T2 and T3 patterns similar; A1, A3, A5, A7 patterns similar; A2, A4, A6, A8 patterns similar except that A8 darker; 2, Second stage; 3, Fifth (mature) stage. L inside circle is true leg; P inside circle is proleg; S inside circle is scolus. Hundreds of small setae not shown. See text for further explanation.

white spots present. *Polygonia satyrus* resembles 1st-stage *zephyrus*, thus head black, T1 mostly white except for black prothoracic shield. BD2 on A2, A4, A6 also yellow-cream; other scoli black, except BD1 on A6 whitish, BD1 on A4 partly whitish, BL1 on A4, A6, A7, A8 mostly white. BD2 on T2, T3, A2, A4, A6 rest on large yellow-cream bumps; other scoli rest on small tan hills, though BD1 on A2, A4, A6, BL1's rest on fairly white bumps. *Polygonia faunus* has enlarged white areas compared to other species, on at least 1 larva BD1 and BD2 on A2, A4, A6 pale. Ventral neck gland occurs in all 3 *Polygonia*.

**Third-stage larva** (Figs. 8, 13, 18). Head black with black scoli, following structures ochre: Mid-dorsal notch, adfrontal cleavage line (lateral to frontoclypeus), lower frontoclypeus, head just above antennae, bases of all major setae except black horns; but some individuals have head mostly black, nearly devoid of pattern. Head setae AG3, PA1, LH1, O2 on long ochre stalks. Body dark brown, with long mostly orange scoli: BL1, BSD1 mostly black; BD2 mostly orange; BD2 on T3, A2, A4, A6 strongly orange; scoli on T2, A10 mostly black. Body pattern similar to stages 4–5.

**Comparison.** *Polygona g. zephyrus* larvae have BD1, BD2 more whitish cream on abdomen. *Polygona satyrus* differs greatly: head black with cream notch on top running



FIGS. 4-15. Leg and cranial setae of *Polygonia prognegrocephalus*. 4, Ventral-medial view of first-stage larval thoracic leg, showing setae typical of butterflies; 5, Setae and olfactory pores of first-stage larval head; 6, Head of second-stage larva. Head horn derived from, or incorporates, seta PA2. Setae PA1, AG3, LH1, O2 arise from small cones on transparent circles of exoskeleton. X's show positions of setae present on some larvae; 7, Head horn of second-stage larva, includes PA2 seta of first stage; 8, Ventral neck gland of larval stages 2-5 partly everted. It appears slitlike when retracted, is fully everted in some preserved larvae; 9, Mandible of first-stage larva; 10, Head setae of fifth-stage (mature) larva with primary setae whose origin is traceable to first-stage larval seta lettered; 11, Labrum of first-stage larval head, anterior view showing one olfactory pore; 12, Labrum of first-stage larval head, posterior view showing two olfactory pores, three spatulate setae; 13, Labrum of third-stage larval head, anterior view; 14, Labrum of fourth-stage larval head, anterior view; 15, Labrum of fifth-stage (mature) larval head, anterior view.

forward to inverted cream V on face, head horns, setae mostly black, some setae on sides and lower face white; body has lateral cream band with cream BL1; top of body cream with cream scoli, black dashes in shape of V without point angling forward from each BD1.

**Fourth-stage larva** (Figs. 8, 14). Head as in mature larva. Body similar to mature larva, but scoli more orangish, BD1, BD2 on A3, A5, A7 with dark brown ring around each above base, whereas other scoli and all scoli on mature larva, lack brown ring.

**Comparison.** The other species also resemble mature larva.

**Mature larva** (Figs. 3, 8, 10, 15, 19, 20, color photo on pl. 3 of Scott 1986). Head black, horns dark brown, orangish cream notch on top, orange-red W on front consisting of streak along upper part of each adfrontal cleavage line plus streak angling down from base of each horn, lower 3rd of frontoclypeus orange-brown, orange-red patch surrounding eye cluster, orangish mottling beside neck. Some setae everywhere on head including AG3, PA1, LH1, O2 orange-red, on long orange stalks; AG2, some dorsal setae beside neck, about 3 lateral setae beside neck on smaller orange stalks. Body scoli ochre, only needle tips orange, except: BD2, BSD1 on T2 black with some orange branches; BD2 on T3 mostly black, orangish on basal 5th, BSD1 ochre; BD2 on A8 partly black, BSD1 mostly black, BD1, BL1 ochre; BD2 on A9 partly black; BD2 on A10 black. Body blackish brown in ground color, with complex pattern. T1 brown with mid-dorsal, subdorsal, suprspiracular, subspiracular orangish lines, some small mostly orange spinelike setae; mid-dorsal ochre band extending from head to T1, narrowing on T2, very narrow on T3. A few ochre transverse dorsal lines between T1, T2, between A8-10. Body joints between

T2, A8 have 5 ochre joint lines, line 2 grayish, lines 1, 3 widest, separated by 4 black joint lines, most posterior very narrow. Segments T2, T3 ochre on top, with paired short black grooves on either side of black mid-dorsal line. Segments A1, A2 similar but paired dark grooves form brown transverse streak behind BD1. A1, especially A2, begin to show dorsal black rearward-aimed V's characteristic of all *Polygonia* on A3-8. Tip of V blunt, wide, corresponding to brown transverse streak on A1-2 just behind BD1, each arm of V thickest in middle anterodorsal to BD2 where V becomes orangish black, outlined by ochre bands as thick as V itself. Three more black spots posterior to point of each V that continue point: black transverse mid-dorsal dash formed by 2 interruptions in 1st black joint line circling segment, narrower dash formed by narrower interruptions in next joint line, mid-dorsal black triangular spot on anterior edge of posterior segment. Ochre joint lines stop at 2 wavy lateral lines characteristic of all *Polygonia*. Upper wavy lateral line orange, on each segment obliquely extending from BSD1, which is ochre with orange base, up, forward then down; behind BSD1 obliquely extending down, backward then down, forward, resembling orange staple aimed down, forward, centered on BSD1. Upper line interrupted between segments by last 3 ochre joint lines which splinter into about 5 ochre wavy narrow lines that stop just above lower wavy lateral line. Lower wavy lateral line ochre, extending from each BL1 obliquely up, forward, then straight forward, then angling down toward BL1 of preceding segment. Beneath this line a vague ochre line above prolegs. Prolegs, underside blackish brown, ochre ventral bands running along abdomen on each side of mid-ventral line. Ventral neck gland present.

Of more than 50 larvae, a few slightly paler (dorsal areas yellow anteriorly, cream behind). Early 5th stage slightly more pinkish violet as orange-red scoli of 4th stage change to ochre.

**Comparison.** California *P. p. oreas*, based on preserved larvae, photos, same as *nigrozephyrus*, except that top front of former orange, yellowish orange vs. orangish yellow on top of thorax, A1-2; BSD1 on orange upper wavy lateral band more orangish than *nigrozephyrus*, ochre in latter with only base orangish. Based on 50-year-old preserved larvae in Smithsonian, ssp. *progne* similar to *nigrozephyrus* in structures, all pattern elements seem present, though impossible to discern true colors; dorsal V-marks, transverse lines between segments present. Edwards (1880) described *progne* color as buff (ochre), dorsal area "reddish" (probably orangish ochre) around black V's; he described T2-3, A9-10 scoli as black, others ochre as in *nigrozephyrus*; described BSD1 as black, but contradicted on the preserved larvae, these being pale also. T1 collar described as yellow in *progne*, and is pale in the preserved larvae, whereas it is black except for mid-dorsal line in *nigrozephyrus*, other 3 species. Head seems to have larger black areas in *nigrozephyrus* than ssp. *progne*. Evidently ssp. *progne* larva does not change color from front to rear as much as western subspecies, and dark brown areas of former are smaller.

Mature larvae of other *Polygonia* species differ greatly. All 3 have black V's on top of abdomen slightly narrower than *nigrozephyrus*, point of each V less strongly connected. All 3 have wavy lower lateral lines as in *nigrozephyrus*, but these are slightly reddish cream in *zephyrus*, red-orange in *faunus*, orangish cream in *satyrus*. *Polygonia g. zephyrus* (Fig. 27, color photo on pl. 2 of Scott 1986) much more 2-toned, top of segments T2-3, A1-2 red-orange, especially T3, A2; top of A3-8 whitish, especially A4, A6 which are yellowish white. Basic pattern elements of *zephyrus* same as in *nigrozephyrus*, but wavy lateral lines weak, slightly reddish, scoli black except BL1 along lower wavy line whitish in some larvae, BD1 orange within orange areas, white within white areas. Head of *zephyrus* also mostly black, except for white mid-dorsal notch, sometimes thin orange inverted V on front, scattered small white seta bases. Some *zephyrus* larvae have T3, A2 orange on top, A4, A6 whitest, whereas in others T2-3, A1-2 equally red-orange on top, A3-8 equally white on top. Latter characteristic of *P. faunus*, which has top of body orange in front, white behind as in photo 14 of *faunus* (= *silvius*) in Pyle (1981). *Polygonia faunus* has both wavy lateral lines red-orange, BL1 on lower line white, head black with some cream setae, cream dorsal notch, orange W on front. Thus mature larvae of *P. g. zephyrus*, *P. faunus* are similar. *Polygonia c-album* L. larvae resemble *faunus* closely (photos in Pyle 1981, Whalley 1979:19, Brooks & Knight 1985:79).

*Polygonia satyrus* mature larvae differ greatly from other *Polygonia* (Fig. 25, color

photo on pl. 2 of Scott 1986). Top near-uniform yellow, same pattern elements present: head black, inverted cream V on front, mid-dorsal cream notch, some small cream setae; middorsal line cream on thorax, transverse rings between segments, dorsal V's present. However, entire top of body greenish yellow, T2-3, A1-2 ochre-yellow in some larvae, lower wavy line thick, pale yellow, orangish between segments in some larvae, yellow BL1's; upper wavy line nearly absent, with black BSD1's or line thin, orange, with cream BSD1's in some larvae.

*Polygonia interrogationis* (Fab.) mature larvae are also very different from other *Polygonia* (Pyle 1981:photo 15, Edwards 1882b). *Polygonia comma* (Harr.) mature larvae vary (Edwards 1882a).

Ventral neck gland present in stages 2-5 of *P. g. zephyrus*, *P. faunus*, *P. satyrus*.

**Chaetotaxy** (Figs. 1-7, 9-15). Head of 1st-stage larva has only primary setae. Second-stage head has many secondary setae, scoli BPA2; each horn incorporates seta PA2 of 1st stage because scoli in same position as 1st-stage PA2, other dorsal primary setae recognizable on 2nd-stage head by large size, position. Each 2nd-stage horn has long PA2 seta on tip, 5 setae on crown below tip. Head setae, horns on stages 3-5 like those of stage 2 except for proliferation of small setae, primary setae recognizable on mature larval head by larger size, horn still including only 1 primary seta, PA2. Setae on labrum constant at 6 on each side, 3 spatulate setae on posterior oral surface, during larval stages 1-5, setae on other mouthparts also constant, except mandible setae which rise from 2 on each stage 1 mandible to about 10 on stage 5.

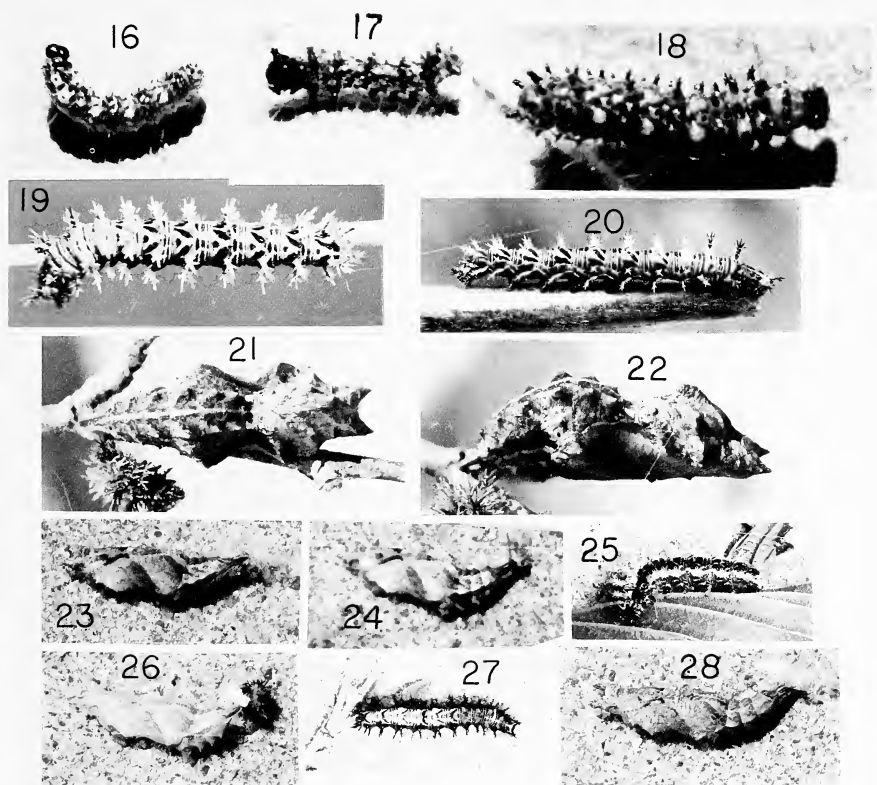
Proprioceptor setae, those that detect cuticular folds telescoping over, on head, body same as present in other Lepidoptera.

Body of 1st-stage larvae has mainly primary setae, also some secondary L2 setae, present on all individuals examined, on T3, A1-8; on A3-6 of some larvae 4th L seta present near L2. On 2nd-stage body, many secondary setae, scoli appear. Body scoli of 2nd-stage larva not homologous with 1st-stage larval primary setae because primary setae of 1st stage occur on 2nd stage, sometimes slightly moved in position, with scoli. Thus A10 of 1st stage has paler spot where BSD1 appears on 2nd stage, yet both stages have same dorsal primary setae on A10; on T2-3, 2nd stage retains same SD, L setae of stage 1 adds BL1; on A8, 2nd stage retains same D1-2, SD1 setae of stage 1, adds BD1, BD2. Body scoli add small setae between stages 2-5, otherwise change little. Small SD plate on T2-3 of stage 2 disappears, only 1 or 2 setae remain on stage 5. Body setae multiply between stages, hundreds of which are not shown on stage 5 setal map (Fig. 3). Crochets typical of butterflies: 14 of anterior 8 prolegs forming circle in stage 1, medial crescent in mature larvae; 12 anal crochets form anteromedial crescent in all stages. Each true leg has 5, 2, 6, 2 tactile setae plus 3, 1, 0, 2 proprioceptor setae on 1st 4 leg segments of stage 1, the usual number in 1st-stage butterflies, additional setae joining these on mature larvae, 1st segment having about 8 setae, for instance, on mature larvae. No anal comb present on any stage.

**Comparison.** Setae, scoli of all larval stages same in 4 *Polygonia* compared, also in mature *P. interrogationis* larvae based on preserved specimens, Petersen (1965) showing drawing of mature *interrogationis* larva: thus secondary 1st-stage L2 seta occurs in all species, L1 on A3-6 in some *zephyrus* individuals splitting into 3 instead of 2 setae, making 4 L's instead of the normal 3, head horn on stages 2-5 incorporating primary seta PA2, consisting of 1 terminal setae, crown of 5 main setae below. Secondary L2 seta on 1st-stage T3-A8 distinguishes *Polygonia* from *Nymphalis*, *Vanessa*.

**Pupa** (Figs. 21-24, color photo on pl. 5 of Scott 1986). Usually pinkish tan, sometimes paler, rarely blackish gray. Segments T3, A1, A2 have silver or gold subdorsal spot, usually silver on T3, A1, often gold on A2 because of reddish tan A2 top, making 6 in all, mid-dorsal silver streak sometimes on A1. Segment A2, to lesser extent A3, reddish tan on top. Four abdominal bands: lateral tan-edged brown band, mid-ventral tan-edged brown band, mid-dorsal brown-edged tan line. Basal half of each tibia brown. Sliver of hindwing just above forewing brown. Light-brown V's on A4-7, weakly on A3, on both sides of tan mid-dorsal line, 1 arm of each V ending at each subdorsal cone. Broad brown, often greenish brown, band crosses wing from tornus to mid-costa, short brown subapical band parallel to it. Many cones, bumps usually at larval scoli positions: very small mid-dorsal





FIGS. 16–28. *Polygonia* larvae and pupae. 16–24 *P. progne nigrozephyrus* from Delta Co., Colorado; 25–28 other taxa as noted from Jefferson Co., Colorado. 16, First-stage larva, dorsal view; 17, Second-stage larva, dorsolateral view; 18, Third-stage larva, dorsal view; 19, Fifth-stage larva, dorsal view; 20, Fifth-stage larva, lateral view; 21, Pupa, dorsal view; 22, Pupa, lateral view; 23, 24, Pupae, lateral views showing variation; 25, *P. satyrus* mature larva, lateral view; 26, *P. satyrus* pupa, lateral view; 27, *P. gracilis zephyrus* mature larva, dorsal view; 28, *P. faunus hylas* pupa, lateral view.

bump on A2–8; large subdorsal cone on T2–3, A1–8; supralateral bump on A3–7; lateral bump on A4–8, lateral bump on each head horn; large bump on wing base; bump on lower basal corner of wing; subventral bump on A5–6, another on head, 1 on each tibia; 2 stout cones (horns) projecting forward from each side of head; mid-dorsal keel on T2. Silk pad spun by pupating larva bright pink.

**Comparison.** All *Polygonia* pupae have similar silver or gold spots in saddle, similar cones, keels, horns, dark bands on abdomen, wings. Species differ in overall color, shape, size of cones, horns. *Polygonia p. oreas* resembles *nigrozephyrus*, but 2 *oreas* pupae seen were brown, not pinkish tan. *Polygonia p. progne* pupa (Edwards 1880) also pinkish brown like *nigrozephyrus*, with similar markings; head, thorax sometimes greenish brown. *Polygonia g. zephyrus* like *nigrozephyrus* in shape, but most individuals light brown, some creamy gray or tinged with green, rarely blackish gray, abdomen more mottled, subdorsal area on A4 lighter than on other segments, on A5–A7 a paler streak angling forward, down from each subdorsal cone. Few *zephyrus* pupae resemble *nigrozephyrus* in overall color, yet reddish tan top of A2 of *nigrozephyrus* identifies most. *P. faunus* pupa (Fig. 28, color photo 14 of Pyle 1981, as *silvius*) light brown (often with reddish



flush on top of A2-3 as in *nigrozephyrus*) or dark gray, easily identified by elongate shape, >10% longer, long head horns, twice as long as other *Polygonia*. *P. satyrus* pupa (Fig. 26, color photo on pl. 5 of Scott 1986) paler, tan or straw, sometimes yellowish dorsally, rarely brown all over, easily identified by mid-dorsal T2 keel being twice as high as other species, subdorsal abdomen cones about twice as large. *P. interrogationis* similar in color to some *nigrozephyrus*, *faunus*, with similar sized bumps, but its T2 keel very large (color photo 15 of Pyle 1981, Edwards 1982b). *P. comma* pupa quite variable (Edwards 1982a). *Polygonia c-album* pupa brown, resembling *nigrozephyrus* in shape but T2 keel larger as in *satyrus* (Brooks & Knight 1985:79).

Oddly, silk cremaster pad spun by pupating larvae colored differently in other species: bright pink in *nigrozephyrus*, also *interrogationis* (photo in Pyle 1981); pale pink in *zephyrus*, *faunus*; yellowish white, rarely faintly pink, in *satyrus*.

#### ACKNOWLEDGMENTS

I thank J. R. Heitzman for larvae of *P. interrogationis*, R. K. Robbins for loans of *Polygonia* immatures from the Smithsonian Institution, P. A. Opler for photos of *P. progne oreas* immatures, and C. F. Gillette for reviewing the manuscript.

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## GENERAL NOTE

### DIFFERING OVIPOSITION AND LARVAL FEEDING STRATEGIES IN TWO *COLOTIS* BUTTERFLIES SHARING THE SAME FOOD PLANT

**Additional key words:** Pieridae, *Colotis amatus*, *C. vestalis*, eggs, Salvadoraceae.

There is much interest in the habit of certain butterfly species laying eggs in clusters. It is generally agreed that cluster-laying is a derived trait, the ancestral butterfly having laid single eggs. Cluster-laying has evolved independently several times in all butterfly families. Its significance has been subject to a variety of interpretations. The purpose of this paper is to present oviposition data for two closely related species of *Colotis* in New Delhi, India.

The species in question are *Colotis amatus* F., whose geographic distribution covers most of Africa, Arabia, India, and Sri Lanka; and *C. vestalis* Butler, found in NW India, Pakistan, and East Africa, but unaccountably absent from Arabia (Larsen, T. B. 1983, Fauna of Saudi Arabia 5:333-478). Together with *C. phisadia* Godart, *C. amatus* and *C. vestalis* form a small section of the genus that feed on Salvadoraceae rather than on the more usual Capparidaceae.

In New Delhi both butterflies feed on *Salvadora persica* L. and *S. oleoides* Decaisne. Usually both are phenologically synchronous, and occur on the same trees or bushes. In size and behavior they are very similar and were not the ground colours salmon and white, respectively, they would be difficult to tell apart on the wing. M. A. Wynter-Blyth (1957, Butterflies of the Indian Region, Bombay Natural History Society, Bombay, 523 pp.) even suggests they interbreed, interspecific copula having been observed.

Given the overall similarity, the difference in oviposition behavior is startling. *Colotis amatus* lays clusters averaging ca. 30 eggs on upper surfaces of fresh leaves at outer extremities of the host plant (Table 1). Eggs are evenly spaced within each clutch. *Colotis vestalis* lays single eggs deep inside the host plant, usually on a twig or a branch, rarely on an old leaf. I observed eggs being laid as far as 90 cm from the nearest leaf, a considerable distance for a small, freshly hatched larva to travel. Larvae of *C. amatus* feed gregariously on fresh foliage, but group cohesion weakens in final instars. Those of *C. vestalis* feed singly on old leaves, usually deep inside the bush or tree. I never found both species on the same leaf.

The egg of *C. vestalis* is chalk white with 20-22 keels extending from the micropyle to the base. It is covered in fine hairs, best visible when the egg is submerged in fluid. Egg volume appeared 15-20% greater than that of *C. amatus*. The latter's eggs are yellow, have only 14-16 keels, lack hairs, and unlike those of *C. vestalis* are covered with a sticky substance. Midges and mosquitoes were often found trapped on egg clutches.

S. Courtney (1984, Am. Nat. 123:276-281) mentions that *Aporia crataegi* L. in Morocco may adjust egg-clutch size to food plant quality. The data are given in more detail by S. Courtney (1986, Adv. Ecol. Res. 15:51-131). *Colotis amatus* clutch-size on the broad-leaved *Salvadora persica* averaged 28.7 eggs ( $n = 106$ ), and on the narrow-leaved *S. oleoides*, 22.7 ( $n = 17$ ) in my Delhi sample; the difference is not statistically significant.

Although these two common butterflies are synchronous and share foodplants, they seem to be noncompetitive. I never saw complete defoliation of food plants. There are a number of potential pathways for two such butterflies to evolve different ovipositing strategies, but data to support any specific hypothesis are not available. Probably no single causal factor underlies all egg clustering. However, available data do not support the hypothesis of R. A. Fisher (1930, The genetical theory of natural selection, Clarendon Press, Oxford, 272 pp.) that egg clustering leads to aposematism; if anything *C. vestalis*, which feeds on old leaves, should be the more aposematic of the two. I masticated a number of specimens without finding the least pungency or emetic response, although I found other aposematic butterflies emetic (Larsen, T. B. 1983, Entomol. Rec. J. Var. 95: 66-67).

The closest parallel I have seen to the two *Colotis* species is that of *Eurema hecabe* L. and *E. blanda* Boisduval in Papua New Guinea and S India. The former lays single eggs,

TABLE 1. Number of eggs in 123 clutches laid in the wild by *Colotis amatus* in New Delhi, India (autumn 1986).

No. eggs in clutch	No. clutches	No. eggs in clutch	No. clutches
1-5	0	41-45	5
6-10	2	46-50	3
11-15	10	51-55	0
16-20	24	56-60	2
21-25	25	61-65	1
26-30	19	66-70	1
31-35	17	71-75	1
36-40	13	76+	0

Average 27.9 eggs per clutch.

the latter clutches. However, in both places the two show more ecological and spatial segregation than *Colotis*; they can feed on the same plants but usually do not do so in the same locality. In Yemen I noticed that Capparidaceae-feeding *Colotis* tend towards local food plant specialisation.

The *Urtica* feeding members of the Vanessini in the Palaearctic fall into two groups. *Vanessa* lay single eggs, *Aglais* lay clutches. Members of both genera are often found on the same batch of nettles, but as in *Colotis* complete defoliation is rare.

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## BOOK REVIEW

THE LIVES OF BUTTERFLIES, by Matthew M. Douglas. 1986. xv + 241 pp. 16 pp. color photographs. University of Michigan Press, Ann Arbor, Michigan, U.S.A. Hard cover. \$45.00.

This attractive book is the product of a scientist and teacher whose enthusiasm is contagious. Its strengths include substantive explanations of many aspects of work on butterfly biology, its discussion of experimental and other evidence for scientific conclusions, and its emphasis on scientific literature. The book is rich in clear, often detailed, explanations of work in several major areas: anatomy, development, and evolution of morphological features of life stages; biophysical, physiological, and ecological constraints on life stages and community structure; behavioral, biochemical and ecological aspects of speciation and coevolution with plants. This exposition is accompanied by many black-and-white diagrams (often from published original drawings or photographs), a section of color photographs illustrating activities and morphological characteristics of life stages, a glossary, several appendices, and a useful index. This combination makes the book an engaging, accessible, self-contained store of information.

In addition, the author enhances the book's informational content in two ways. First, he places specific examples in a conceptual context by discussing considerations that underlie specific hypotheses. Explanations of how observations and experimental data are collected contribute to a clear sense of how scientific questions are raised and examined, and why "answers" may be open to alternative interpretations. This aspect of the book reflects the author's experience as a university professor; many of his discussions would make good lecture notes for an advanced undergraduate course. This bold focus on processes of scientific research may be the book's most important contribution to its educational goals. Second, the book's emphasis on recent research literature provides a resource for further study.

The question of readership presents problems for the book. While ostensibly written for an audience that has some background in biology, its attempt to appeal to both lay and professional audiences sometimes creates disconcerting inconsistencies. For example, the author describes "sex-limited mimicry" as a special case of Batesian mimicry in which one sex mimics unpalatable models; he includes a definition of this term in the glossary. Ten pages later, however, "sex-limited" is used colloquially to describe distribution of a trait whose pattern of inheritance is sex-linked. This colloquial use of a term that has specific meaning in genetics is confusing. Similarly, the author emphasizes his personal research experience in a way likely to engage the interest of lay readers. To a professional readership, however, such emphasis is likely to seem egotistical and annoying.

This book thus attempts the dual challenges of engaging and educating a lay readership as well as concisely reviewing recent literature for a professional audience. This is a rarely attempted goal, and the author presents us with a unique solution. The book's value to its potential professional audience lies in its conciseness and timely review of much recent literature. Its appeal to this audience is uncertain, because professors whose students study these research topics in class may assign the original literature rather than this book. However, the author's contribution to explicating butterfly biology and scientific research for a lay audience is a noteworthy success.

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## OBITUARY

### ABNER ALEXANDER TOWERS (1916-1987): A Tribute

The Lepidopterists' Society lost one of its charter members with the passing of Abner A. Towers, who was well-known to collectors in the Southeast and to participants in the first of the collecting expeditions to Ecuador organized by Thomas C. Emmel and Giovanna Holbrook.



Abner Alexander Towers

Born in Gadsden, Alabama, 28 January 1916, Abner Towers developed an interest in wildlife as a boy, particularly his lifelong fascination with butterflies and moths, birds, and other flying creatures. He grew up in Gadsden, completing his primary schooling there, then attended the Kent School, in Kent, Connecticut, during which time he began to collect and study Lepidoptera seriously. At the age of eighteen, in 1934, he took his first trip to the Florida Keys expressly to observe and collect butterflies and moths. He attended the Massachusetts Institute of Technology as a general science major, and, after earning the Bachelor of Science in 1939, served as an officer in the U.S. Army Corps of Engineers. He spent most of World War II in the Aleutian and Philippine Islands. Following the war he settled in Georgia, the state he would call home for the rest of his life. Abner Towers married, raised a family, and built a career as an engineer and chemist, and was often described in both capacities by co-workers and peers as "brilliant." In August 1972, he cofounded A-Jay Chemical Company, in Powder Springs, Georgia, an industrial chemical firm he continued to administer until his terminal illness.

In the 1950's Abner resumed his study of the Lepidoptera of the region, focusing his attention almost entirely on the butterflies of Georgia and Florida, and he steadily built an impressive collection containing substantial series of virtually all the species recorded from the two states. He established a strong friendship with Lucien Harris Jr., and his contributions to Harris's *The Butterflies of Georgia* (University of Oklahoma Press, 1972) were significant, and included numerous state records and field observations. Abner's



persistent and dedicated collecting subsequently added several species to the Georgia butterfly fauna, including *Mitoura hesseli* Rawson & Ziegler, and, in 1981, he participated in the discovery of a new geometrid, described as *Narraga georgiana* Covell, Finkelstein & Towers (J. Res. Lepid. 23:161-168, 1984). Occasionally, when his other responsibilities allowed, Abner traveled and collected outside the country; most notable were his collecting trips to Ecuador in 1980 and Jamaica in 1982.

Abner Towers died 18 March 1987, after a bravely fought three-year battle with leukemia. He is survived by his wife, Margaret Le Craw Towers, his children John A. Towers, Marsha Towers Endictor, and Andrea Towers Rohaly, and his sister Harriet Towers Bjelouvucic. His friends and co-workers remember him as "a man of warmth . . . who always took time to inquire of people's families, discuss their hobbies, jobs or personal interests and give advice, if asked, with a sincerity derived from a love of people. He was totally unselfish with his time, his knowledge and his abilities." (From a eulogy by Alan Shipp and Polly Buford.)

His collection was donated to the University of Florida in 1985 and deposited in the Florida State Collection of Arthropods, Gainesville. In addition to the Lepidopterists' Society, Abner was a charter member of the Southern Lepidopterists, a group he served since its founding in 1978 as Georgia zone coordinator.

"Abner Towers was a gentle man, and a gentleman. He will be missed." (Shipp and Buford.)

IRVING L. FINKELSTEIN, 425 Springdale Drive N.E., Atlanta, Georgia 30305.







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# JOURNAL

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**Cover illustration:** Mature larva of *Papilio polyxenes asterius* Stoll on wild carrot, *Daucus carota* L. Submitted by John V. Calhoun.

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## IMPACT OF OUTDOOR LIGHTING ON MOTHS: AN ASSESSMENT

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**ABSTRACT.** Outdoor lighting has sharply increased over the last four decades. Lepidopterists have blamed it for causing declines in populations of moths. How outdoor lighting affects moths, however, has never been comprehensively assessed. The current study makes such an assessment on the basis of published literature. Outdoor lighting disturbs flight, navigation, vision, migration, dispersal, oviposition, mating, feeding and crypsis in some moths. In addition it may disturb circadian rhythms and photoperiodism. It exposes moths to increased predation by birds, bats, spiders, and other predators. However, destruction of vast numbers of moths in light traps has not eradicated moth populations. Diverse species of moths have been found in illuminated urban environments, and extinctions due to electric lighting have not been documented. Outdoor lighting does not appear to affect flight or other activities of many moths, and counterbalancing ecological forces may reduce or negate those disturbances which do occur. Despite these observations outdoor lighting may influence some populations of moths. The result may be evolutionary modification of moth behavior, or disruption or elimination of moth populations. The impact of lighting may increase in the future as outdoor lighting expands into new areas and illuminates moth populations threatened by other disturbances. Reducing exposure to lighting may help protect moths in small, endangered habitats. Low-pressure sodium lamps are less likely than are other lamps to elicit flight-to-light behavior, and to shift circadian rhythms. They may be used to reduce adverse effects of lighting.

**Additional key words:** conservation, evolution, flight, urban ecology, light pollution.

Since the invention of the incandescent lamp over a hundred years ago, outdoor lighting has progressively increased. The growth has been characterized by expansion into new geographic areas, development of new lamps with new spectral characteristics, and increases in total amount of light and radiant energy (Riegel 1973, Hendry 1984, Sullivan 1984). Outdoor lighting has transformed the nocturnal face of the earth (Croft 1978). However, despite universal awareness that electric light disturbs behavior of nocturnal insects, the ecological impact of outdoor lighting has never been comprehensively assessed.

The possibility that outdoor lighting may adversely affect our fauna

is well recognized. Lepidopterists have blamed outdoor lighting for declines in populations of North American moths, especially saturniids in the northeastern United States (Holland 1903, Ferguson 1971, Hessel 1976, Muller 1979, Worth & Muller 1979, Krivda 1980, Pyle et al. 1981). This view assumes a direct causal link between lamps and faunal change. Fundamental questions about such a link, however, have never been closely examined: What mechanisms might link lamps with changes in populations of moths? If lamps cause populations of moths to change, specifically what might the changes be? How important are effects of lighting compared to effects of other environmental disturbances? This study examines each of these questions. It investigates the hypothesis that outdoor lighting influences populations of moths.

The investigation is based on a review of literature. The presentation is organized into three sections. The first section describes distribution, growth, energy, and spectral composition of outdoor lighting. The second describes how lamps affect behavior, life functions and survival of individual moths. The third explores how such effects may disturb moth populations; it also discusses measures to reduce disturbances caused by lighting. Citations are deliberately extensive to facilitate retrieval of source material which is widely scattered among different disciplines.

### LIGHTING

Nocturnal images of earth viewed from orbiting satellites show the distribution of outdoor lighting (Fig. 1). In the United States this distribution coincides with that of the country's population (Croft 1978). Nocturnal illumination is clustered around all large metropolitan areas, with greatest concentration in the Northeast corridor. Viewed from an airplane, nocturnal lighting delineates a web of interconnecting roadways lined with illumination from houses, parking lots, billboards, and other landmarks. Such aerial observation suggests that lighting forms an illuminated web that envelops the nocturnal environment of Lepidoptera. The web's density varies with human population density, and its distribution is continental.

The magnitude of lighting in a major metropolitan area is illustrated by Philadelphia's streetlighting (Table 1). Philadelphia has 100,000 high-pressure sodium streetlamps at a density of almost 300 lamps/km<sup>2</sup>. The energy they radiate equals more than 10 kilowatts/km<sup>2</sup>, an order of magnitude greater than the energy density of moonlight at full moon (Agee 1969). During the last 4 decades, lamp size (lumens) increased 7-fold, number of lamps tripled, and type of lamp changed from tungsten filament and mercury to high-pressure sodium (Figs. 2 & 3) (Wainwright 1961, C. A. Oerkvitz pers. comm.). Nationwide per capita consumption of electrical power for streetlighting is similar to that of





FIG. 1. Composite image of nocturnal United States, as viewed from orbiting satellite in fall 1985 (Defense Meteorologic Satellite Program). Photograph from National Snow and Ice Data Center, Campus Box 449, University of Colorado at Boulder, Boulder, Colorado 80309.

TABLE 1. Streetlamps in Philadelphia, 1983. Total lamps, lumens, and demand (watts) from C. A. Oerkvitz (pers. comm.). Radiant energy calculated from GTE Products Corp. (Sylvania) (1977b). Demographic data from *World Almanac* (1986).

Streetlamp parameter	Number		
	Total	Per capita	Per km <sup>2</sup>
Lamps	1.0 × 10 <sup>5</sup>	5.8 × 10 <sup>-2</sup>	2.8 × 10 <sup>2</sup>
Lumens	1.8 × 10 <sup>9</sup>	1.1 × 10 <sup>3</sup>	5.0 × 10 <sup>6</sup>
Radiant energy (watts) emitted for wavelengths 350–700 nm	5.6 × 10 <sup>6</sup>	3.3	1.6 × 10 <sup>4</sup>
Electric power demand (watts)	2.2 × 10 <sup>7</sup>	1.3 × 10	6.1 × 10 <sup>4</sup>

Philadelphia, and growth in lumens has been comparable or higher (Riegel 1973, Edison Electric Institute 1971, 1985, Sullivan 1984).

Conversion from mercury to high-pressure sodium lamps reduces radiant energy at the short-wavelength end of the spectrum. However, high-pressure sodium light is spectrally broad and does include radiant energy in the blue spectral region (Fig. 2B).

In contrast to high-pressure sodium light, low-pressure sodium light is spectrally narrow. It excludes practically all energy in the ultraviolet, blue, and green regions of the spectrum (Fig. 2A). Viewed through a spectroscope, its spectrum contains a bright yellow-orange line (actually 2 spectral lines very close together) near 589 nm. Because the human eye is particularly sensitive to light in the 589 nm region, low-pressure sodium lamps can provide bright illumination with comparatively little radiant energy (Finch 1978). Compared to other lamps used for outdoor lighting, low-pressure sodium lamps minimize environmental exposure to radiant energy both in number of wavelengths and number of watts. These lamps are used for streetlighting and other outdoor lighting, but much less frequently than are high-pressure sodium lamps.

Conversion of streetlamps from mercury to high-pressure sodium has changed the spectral distribution of outdoor lighting, but it has not changed it as much or as clearly as one might suppose. Mercury lamps, for example, are still used for residential and commercial lighting in Philadelphia, and for streetlighting in neighboring areas. Tungsten filament (Fig. 3), low-pressure sodium, metal halide (Fig. 2C) and fluorescent lamps (Sorcar 1982) all contribute to spectral diversity of outdoor lighting in the city. While density and distribution of outdoor lighting have increased, spectral composition has diversified.

EFFECTS ON INDIVIDUAL MOTHS

Vision

Bright light can lower sensitivity of moth eyes 1000-fold (Bernhard & Ottoson 1960a, Höglund & Struwe 1970, Agee 1972, 1973, Eguchi

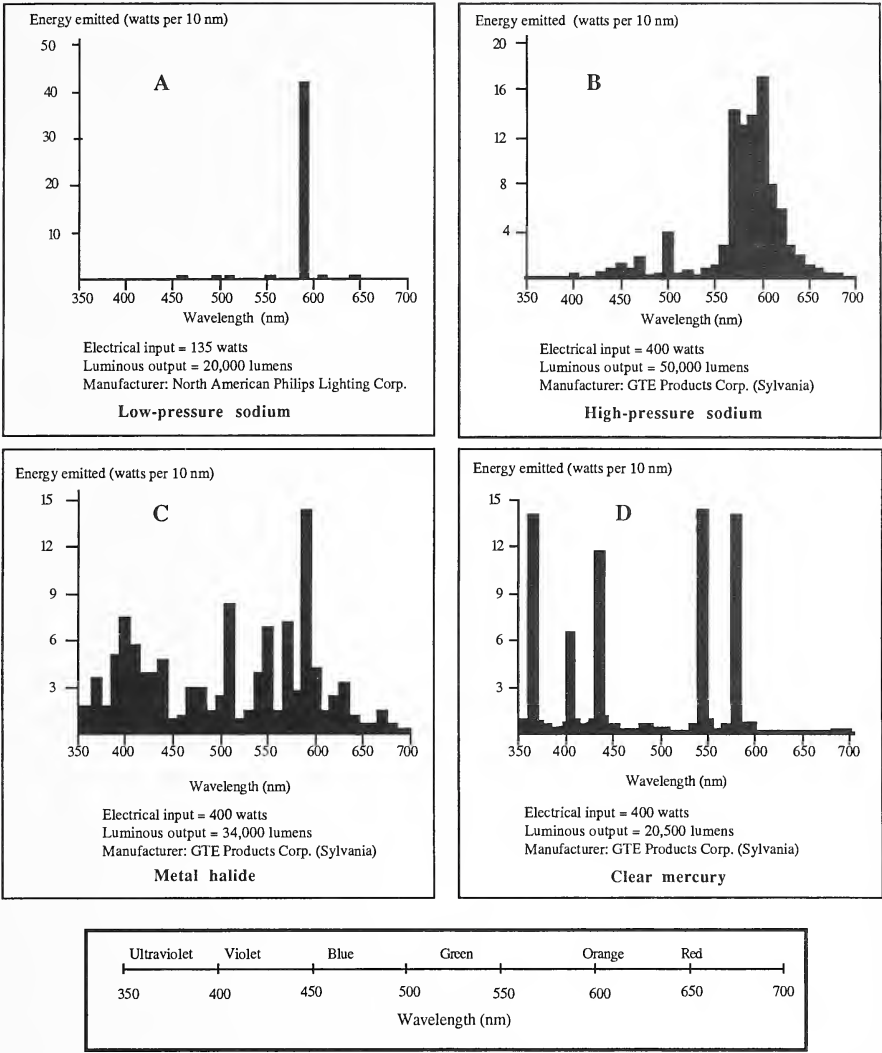
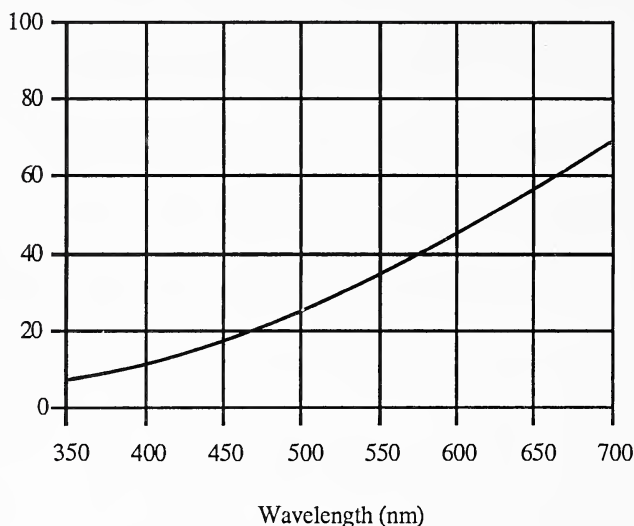


FIG. 2. Spectral energy distribution of vapor discharge lamps. Sources for A: Judd 1951, Finch 1978, Illuminating Engineering Society 1981, North American Philips Lighting Corp. 1982. Sources for B, C, and D: GTE Products Corporation (Sylvania) 1977a, 1977b, 1979.

& Horikoshi 1984). Electroretinographic studies suggest what happens to the visual sensitivity of a moth that flies to a lamp. If the moth remains at the lamp and then flies away, full visual sensitivity may not return for 30 min or longer (Bernhard & Ottoson 1960a, 1960b, Agee 1972). This effect requires exposure to the lamp over a period of time, probably 10 min or longer (Day 1941, Höglund 1963, Yagi & Koyama

Relative energy



Electrical input: 1000 watts  
Luminous output: 23,100 lumens  
Color temperature: 3030° Kelvin

FIG. 3. Spectral energy distribution of tungsten filament ("incandescent") lamp. Sources: GTE Products Corporation 1972, 1974.

1963). A moth flying away from a lamp into relative darkness on a cloudy, moonless night may be functionally blind until enough time has elapsed for it to become fully dark-adapted.

Continuous exposure to bright electric lamps could in theory "dazzle" moths. This means it could stimulate the moth retina so intensely that the retina could not respond to additional increases in light. The result would be functional blindness so long as the moth remained exposed close to the lamp. Electroretinographic evidence, however, suggests that lamps do not dazzle moths (Eguchi & Horikoshi 1984).

Net effects of electric lighting on moth vision may vary according to local conditions as well as moth behavior. Urban lighting increases background illumination which in turn may help moths see. Electric lighting in some areas has increased nocturnal sky brightness as much as 20-fold (Hendry 1984). However, the spectral composition, polarization and spatial distribution of outdoor lighting varies widely in different settings. In some locations they may differ so much from that of natural nocturnal light that they create visual artifacts and distortions. One

outcome of disturbed vision is flight to outdoor lamps, but many disturbances in visual function and behavior are possible.

The suggestion that urban lighting influences nocturnal vision of moths may appear paradoxical. Municipal light sources have shifted away from mercury lamps and toward high-pressure sodium lamps. One might suppose that moth retinas are insensitive to the relatively long wavelengths which characterize most of the energy contained in high-pressure sodium light (Fig. 2B). Moths, for example, do not fly to the 589 nm light of low-pressure sodium lamps (Fig. 2A), or do so rarely (Robinson 1952). Such a supposition, however, is incorrect: electroretinograms of moths consistently demonstrate sensitivity to light in the 589 nm region, and most studies have found maximum sensitivity in the green rather than ultraviolet part of the spectrum (Jahn & Crescitelli 1939, Höglund & Struwe 1970, Hsiao 1972, Mikkola 1972, Agee 1973, MacFarlane & Eaton 1973, Langer et al. 1979, Mitchell & Agee 1981, Eguchi et al. 1982). Retinal sensitivity extends farther into the long-wavelength end of the spectrum than flight-to-light behavior typically would suggest (Mikkola 1972, MacFarlane & Eaton 1973, Mitchell & Agee 1981).

### Navigation

**Diversion to lamps.** Three hundred fifty-six species of Macrolepidoptera, or about a third of those species found in all of Great Britain, were collected at a single light trap in England (Williams 1939). Comparable findings have been reported in Britain and North America (Dirks 1937, Robinson & Robinson 1950a, Beebe 1953, Bretherton 1954, Moore 1955, Langmaid 1959, Hosny 1959, Holzman 1961, Moulding & Madenjian 1979). Tens of thousands of moths have flown to a single lamp in a single evening (Robinson & Robinson 1950a), and huge swarms of moths have aggregated around urban light sources (Howe 1959). On the other hand, some species of nocturnal moths rarely fly to lamps even though large populations of them may be flying nearby (Bretherton 1954, Taylor & Carter 1961, Janzen 1983). A variety of physiologic, behavioral and environmental factors may determine which species of moths fly to light and when (Geier 1960, Gehring & Madsen 1963, Milyanovskii 1975, Mazokhin-Porshnyakov 1975, Janzen 1983, 1984).

Large numbers of moths flying to lamps may give a false impression that lamps divert moths from great distances. Effective radius of a 125-watt mercury vapor light trap was initially reported to be 91 m, but later estimates reduced the figure to 17 m, and the most recent analysis cut the distance to 3 m (Robinson & Robinson 1950a, Robinson 1960, Baker & Sadovy 1978). Other studies have shown flight-to-light dis-



tances of 10 m or less (Stanley 1932, Hamilton & Steiner 1939, Hartstack et al. 1971, Plaut 1971). Long-distance estimates ranging up to half a kilometer represent either extrapolation, artificial conditions or both (Graham et al. 1961, Hsiao 1972, Agee 1972, Stewart et al. 1969, Plaut 1971, Bowden & Morris 1975).

If the mechanism by which a lamp disturbs moths depends on diversion of flight paths to the lamp, then the moths disturbed must be limited to those flying in the geographic area immediately adjacent to the lamp. In this sense any direct effects of a particular lamp would tend to be local, except when topography (Beebe 1949, Beebe & Fleming 1951), foodplants, pheromones, or other factors concentrate moths near the lamp. Only in urban regions would density and distribution of lamps be great enough to influence large populations of moths over broad geographical areas.

Effects of electric lamps in urban areas, however, may be much smaller than one might expect. Robinson & Robinson (1950a) noted that lamps in isolated phone booths appear to be much more effective in eliciting flight-to-light behavior than are clusters of bright urban lamps located immediately adjacent to areas with large populations of moths. They demonstrated that lamps interfere with each other's capacity to elicit flight-to-light behavior, and the closer together the lamps, the greater the interference. The high density which characterizes distribution of urban lamps suppresses flight-to-light behavior.

Urban lighting may suppress flight to light for a number of reasons. Light trap collections vary with the lunar cycle and are lowest at full moon (Williams et al. 1956, Agee et al. 1972, Nemec 1971, Dufay 1964, Bowden & Church 1973, Janzen 1983, Stradling et al. 1983). A similar correlation with moonlight cannot be demonstrated when nocturnal flight is measured by suction traps (Williams et al. 1956, Danthana-rayana 1986), pheromone-baited traps (Saario et al. 1970, Janzen 1984) or radar (Schaefer 1976). Moths active at dusk typically appear in suction traps before they appear in light traps (Taylor & Carter 1961). Eye pigment must be in a position of dark adaptation before moths will fly to light (Collins 1934), and even relatively dim background light can cause the pigment to move away from this position (Bernhard & Ottoson 1964). Diffuse urban light, like moonlight and twilight, reduces the darkness essential for flight-to-light behavior.

The moon not only increases background lighting but also constitutes a concentrated source of light by which insects may be able to orient (Sotthibandhu & Baker 1979). Moths flying by lunar navigation may bypass lamps (Baker & Sadovy 1978). Lamps may provide navigational cues which suppress flight to other lamps.

Light sources that emit large amounts of ultraviolet energy are gen-

erally most effective in eliciting flight-to-light behavior (Williams et al. 1955, Glick & Hollingsworth 1955, Klyuchko 1957, Deay et al. 1965, Mazokhin-Porshnyakov 1969, 1975, Mikkola 1972, Sargent 1976, Mitchell & Agee 1981). Conversion of mercury streetlamps to high-pressure sodium and metal halide streetlamps has undoubtedly tended to reduce flight to streetlamps. On the other hand, moths do fly to high-pressure sodium and metal halide lamps, and a small minority of species may fly preferentially to lamps with little or no ultraviolet emission (Klyuchko 1957, Mikkola 1972). Unlike high-pressure sodium lamps, however, low-pressure sodium lamps rarely elicit flight-to-light behavior (Robinson 1952).

In summary, increases in electric lighting do not necessarily impair nocturnal vision and navigation. Under some conditions they may improve moths' nocturnal vision and suppress flight-to-light behavior.

**Diversion away from lamps.** Electric lamps may also divert moths away from them (Robinson & Robinson 1950a, Robinson 1952, Herms 1929, 1932, Nomura 1969, Nemec 1969, Hsiao 1972). These effects may depend in part on spectral output of the lamp (Mazokhin-Porshnyakov 1969, 1975, Nomura 1969). Several theories attempt to explain this behavior (Hsiao 1972), but none accounts for diversity of flight paths at lamps (Janzen 1984): while some moths make spiral or circular flights around lamps and land several meters away, others make a beeline straight to lamps and crash into them. Flight paths approaching lamps may zig-zag or be totally chaotic (Holzman 1961, Mazokhin-Porshnyakov 1969, Janzen 1984). Diversion away from lamps has been debated (Bretherton 1950, Robinson & Robinson 1950b). Evidence that moths avoid large illuminated areas (Herms 1929, 1932, Nomura 1969, Nemec 1969) is inconclusive, but this behavior is more difficult to demonstrate than flight to lamps.

Lamps suppress flight of moths that fly to them. Moths approaching lamps may land near them and remain quiescent for a moment or for the entire night. Lamps suppress flight of some species more than others (Blest 1963, Graham et al. 1964). In some cases lamps do not appear to suppress flight; in other cases they excite quiescent moths into flight (Collins 1934, Hsiao 1972). Diurnal moths occasionally fly at night to lamps (Engelhardt 1946, Janzen 1983), but here it is unclear whether the lamps help to initiate nocturnal flight.

Diversion and suppression of flight may impair orientation and navigation based on lunar, stellar or other visual celestial cues (Mazokhin-Porshnyakov 1969, Sothibandhu & Baker 1979, Wehner 1984) including polarization of celestial light (Danthanarayana & Dashper 1986). It also may impair navigation and orientation based on geomagnetic, gravitational, barometric, aerodynamic, inertial, olfactory, acoustic or

visual terrestrial cues (Baker & Kuenen 1982, Baker & Mather 1982, Janzen 1984, Schöne 1984, Riley & Reynolds 1986). How much electric lighting disturbs use of particular cues may be expected to vary in part according to which cues the moth happens to be using at the moment it encounters the lamp.

### Migration and Dispersal

Light sources divert moths engaged in migratory or dispersal flights (Cockerell 1914, Williams 1937, Beebe & Fleming 1951, Wolf et al. 1986). Urban lighting surrounds habitats isolated by urban sprawl, so that moths may have to traverse dozens of kilometers of densely illuminated territory to arrive at potential breeding sites. Moths flying high (Glick 1965) may fly to urban light sources on tall buildings (Stanley 1932, Glick 1961). Because location of natural flyways is poorly documented for North American moths, one cannot determine the extent urban lighting may intersect long-range natural migration routes here. In Venezuela, vast numbers of migrating moths aggregated around lamps near a narrow mountain pass which functions as a natural flyway (Beebe 1949, Beebe & Fleming 1951). Lighting along roads following topographical features such as valleys, rivers, and coastlines might selectively interfere with North American moth migrations (Fig. 1).

### Oviposition

Electric lighting can disturb oviposition. Light-trap surveys have shown that the vast majority of females collected at lamps are gravid (Dirks 1937, Ficht et al. 1940, Glick & Hollingsworth 1954, Geier 1960, Gehring & Madsen 1963) although males usually outnumber them (Dirks 1937, Williams 1939, Sargent 1976, Worth & Muller 1979, Janzen 1984). Flight to light can shift oviposition to sites located near the lamp (Ficht et al. 1940, Martin & Houser 1941, Pfrimmer & Lukefahr 1955, Beaty et al. 1951, Nemec 1969, Brown 1984). Eggs may be deposited on lampposts, window screens, buildings, and other unsuitable sites near lamps. Egg densities may be several-fold higher on plants near lamps (Martin & Houser 1941). The result may be larval overcrowding and increased susceptibility to starvation, microbial infection, and predation.

Lamps shift the distribution of oviposition sites toward them probably by diverting ovipositing females and not by stimulating oviposition. In cornfields, *Ostrinia nubilalis* (Hbn.) (Pyralidae) tends to oviposit near lamps (Ficht et al. 1940, Beaty et al. 1951), but in the laboratory nocturnal illumination suppresses *O. nubilalis* oviposition (Skopik & Takeda 1980). Similar observations have been reported in *Pectinophora gossypiella* (Saund.) (Gelechiidae) (Pfrimmer & Lukefahr 1955, Lu-

kefahr & Griffin 1957, Henneberry and Leal 1979). Outdoor lighting may decrease oviposition by *Cydia pomonella* (L.) (Tortricidae) and *Heliothis* spp. (Noctuidae), although the mechanism is unclear (Hermes 1929, 1932, Nemec 1969).

### Mating

Outdoor lighting does not prevent mating in certain Saturniidae: male *Hyalophora cecropia* (L.) and *Samia cynthia* (Drury) complete long-distance mating flights to virgin females at night across illuminated urban territory, and breed in urban habitats (Rau & Rau 1929, Pyle 1975, Sternburg et al. 1981, Waldbauer & Sternburg 1982). Most freshly emerged female saturniids do not fly at all until they have emitted pheromone and mated (Blest 1963, Nässig & Peigler 1984, Waldbauer & Sternburg 1979). Male sphingids and saturniids fly to virgin females before they fly to nearby electric lamps (Allen & Hodge 1955, Worth & Muller 1979, Janzen 1984). Almost all female *Cydia pomonella* collected at black lights have already mated (Gehring & Madsen 1963). Although more males than females typically fly to lamps, the capacity of males to mate with more than one female (Rau & Rau 1929, Allen & Hodge 1955, Lukefahr & Griffin 1957, Vail et al. 1968) may moderate the reproductive impact of disproportionate harm to males.

In contrast, electric lighting may have a major effect on mating in certain Noctuidae. *Heliothis zea* (Boddie) is an example. The peak time of night during which *H. zea* flies to light traps coincides with the period of copulation (Graham et al. 1964, Stewart et al. 1967). Only a third to a half of female *H. zea* collected at light sources have mated (Gentry et al. 1971, Vail et al. 1968). In the laboratory, *H. zea* will not mate unless its eyes are in a state of dark adaptation, as indicated by the presence of eye glow. Light intensity must be below  $0.015 \mu\text{W}/\text{cm}^2$ , the intensity of light of a quarter-moon (Agee 1969). The suggestion is that *H. zea* females fly to light sources whose radiant energy suppresses mating.

A criticism of this scenario is that unmated *H. zea* females that fly to light may be migrating (Raulston et al. 1986) and therefore sexually immature (Johnson 1969). Female *H. zea* in the laboratory do not mate for 30–60 h after eclosion (Agee 1969). However, even if unmated females at lamps were sexually immature migrants, the lamps could disrupt reproductively important behavior, such as flight to locations where courtship and mating would be likely to occur. Furthermore, outdoor lighting may interfere with *H. zea* mating regardless of flight to light. Levels of light that suppress mating in the laboratory (Agee 1969) are well below ambient levels of light in electrically illuminated environments outdoors. Low levels of incandescent light (Nemec 1969)



and moonlight (Nemec 1971) have influenced activities of *Heliothis* spp. in the field.

Other evidence suggests that lighting may interfere with mating. Unmated females of four other noctuid species fly to lamps (Vail et al. 1968). Male sphingids caught in light traps baited with virgin females do not seek out the females (Hoffman et al. 1966). In the laboratory, even dim electric light (0.3 lux) suppresses female *Trichoplusia ni* (Hbn.) (Noctuidae) pheromone release and male response to pheromone (Shorey & Gaston 1964, 1965, Sower et al. 1970). Electric light also suppresses female pheromone release and male response to pheromone in *Dioryctria abietivorella* (Grt.) (Pyralidae) (Fatzinger 1979). Mating by *Pectinophora gossypiella* requires a period of relative darkness lasting at least 7 h (Lukefahr & Griffin 1957).

### Feeding

Moths may feed in illuminated environments. Sphingids and noctuids visit food sources in full view of electric lamps located sometimes less than a few meters away, or they fly to electric light sources after they have completed feeding (Bretherton 1954, Milyanovskii 1975, Mazokhin-Porshnyakov 1975, Janzen 1983, 1984). I have observed *Buddleja* (Gentianaceae) blossoms covered with noctuids at night (2300 h) virtually directly under a tungsten filament street lamp illuminating a heavily traveled road in Quisset, Massachusetts. Light from automobile headlights and from a flashlight did not alter the moths' activities.

Electric lamps, however, may interfere with feeding. Orchard illumination has reduced the number of *Cydia pomonella* feeding at bait (Herms 1932). In Japan, orchard illumination has been used to protect fruit from damage by fruit-piercing noctuids (Nomura 1969). Light has disturbed nectaring sphingids (Brown 1976). Diversion of moths away from light may explain why lamps interfere with feeding. Suppression in feeding is moot for the large number of moth adults that never feed (Norris 1936).

Electric lighting theoretically could injure larval foodplants. Sodium vapor lighting may harm plants by disrupting photoperiodic regulation of growth and development (Sinnadurai 1981, Cathey & Campbell 1975, Shropshire 1977), but such effects are apparently greater indoors in greenhouses than outdoors on the street (Andresen 1978).

### Time Keeping

Electric lighting can delay or advance vital activities of moths and their larvae, and these shifts could affect the insects as much as changes in the activities themselves (Beck 1980, Saunders 1982). This possibility has been the basis for proposals to exploit biological clocks for purposes



of pest control (Barker et al. 1964, Nelson 1967). In a field trial, however, light exposure failed to prevent diapause in larvae of *Adoxophyes orana* (F.R.) (Tortricidae) (Berlinger & Ankersmit 1976). The trial suggests that it is easier to manipulate biological clocks indoors than outdoors where temperature and other factors cannot be controlled.

Biological clocks of flying insects, however, may be much more susceptible to outdoor electric lighting than those of larvae. This is because flight to light increases exposure to radiant energy. Exposure to a pulse of light lasting only 15 min is sufficient to attenuate a circadian rhythm in *Drosophila*; light  $10^3$  times more intense produces the same effect after only 10 sec; light  $10^5$  times more intense does it after an exposure of less than 0.1 sec (Chandrashekar & Engelmann 1976). Energy for even a minute fraction of a second (photoflash) can disturb photoperiodic clocks in larvae of Lepidoptera (Barker et al. 1964). The anthropomorphic observation that quiescent moths adjacent to a lamp are "asleep because they think it is daytime" may be close to the truth.

Shifts in timing of nocturnal behavior of moths at lamps do not necessarily imply shifts in phase of endogenous rhythms. Changes in timing of behavior could represent other responses to light, or they could represent complex mixtures of responses. Regardless of these possibilities, magnitude and character of responses may vary according to when in the circadian cycle exposure to light occurs (Pittendrigh & Minis 1971, Skopik & Takeda 1980). Responses may also vary depending on spectral output of the lamp. For example, *Pectinophora gossypiella* has two light-sensitive clocks, only one of which responds to the 589 nm light emitted by low-pressure sodium lamps (Bruce & Minis 1969, Pittendrigh et al. 1970).

### Theoretical Effects

To what extent nocturnal flight to light affects timing of nocturnal behavior has never been formally investigated. For example, if a moth flies to a light source, receives intense irradiation for 15 min, and flies away, how will its activities during the rest of the night be affected? If a male, will its mating period still coincide with that of females not exposed to light? If a female, will pheromone release still occur during the flight period of males? Shifts in mating times could cause sympatric, closely related species to attempt to mate with each other; such species normally do not mate with each other in part because their different mating periods keep them temporally segregated (Tuttle 1985).

Synchronization of activities with lunar rhythms may help moths navigate, mate, and avoid predators (Danthanarayana 1986). Lamps may disturb oviposition synchronized to lunar rhythms (Nemec 1969, 1971). To what extent moth activity synchronizes with lunar rhythms,

and to what extent electric lighting may disturb such synchrony warrants investigation.

### Predation

Bats, birds, skunks, toads, and spiders hunt moths flying to lamps (Stanley 1932, Thaxter 1957, Holzman 1961, Krivda 1980, Covell 1985, Brower 1986). Lamps increase predation by clumping prey, and directly exposing them to attack (Turnbull 1964). Concentrated experience with particular species may help birds learn to defeat defenses based on surprise, novelty, or deceit (Blest 1957, Wickler 1968, Coppinger 1970, Sargent 1973b, Pietrewicz & Kamil 1979). Lamps also can destroy defensive behavior, such as that required for crypsis (Sargent & Keiper 1969, Sargent 1973a, 1976). The outcome is exemplified by a dark, bark-colored moth conspicuously resting on a white wall near a lamp at dawn. Lamps may help birds learn to recognize unpalatable species, but moths unpalatable to some birds may be acceptable to others (Löhrl 1979). Lamps may enable different birds to pick and choose among different possible prey. Because moths often land before they arrive at lamps, lamps may provide predators with far more prey than one might expect from the moths immediately adjacent to the lamp (Hartstack et al. 1968).

Parasitoids of Lepidoptera fly to electric light sources (Collins & Nixon 1930, Cline et al. 1983). Electric lighting could reduce predation on Lepidoptera by suppressing populations of parasitoids (Worth & Muller 1979). It may divert parasitoids used for biological control of pest Lepidoptera in warehouses (Cline et al. 1983). Even brief exposure to intense sources of radiant energy (photoflash) may sterilize minute hymenopterous parasites which survive the radiation (Riordan 1964). Theoretically, lighting could affect secondary parasites, thus potentially disturbing the food chain at three levels, and producing changes in populations which would be difficult to predict (Frank 1986).

## EFFECTS ON MOTH POPULATIONS

### Evidence Against Effects

**Migration and dispersal.** Even though lamps may contribute to the destruction of vast numbers of moths, the impact on moth populations may be negligible. For example, more than 10 000 *Autographa (Plusia) gamma* (L.) (Noctuidae) were collected in a light trap in one season in England (Robinson & Robinson 1950a). In England the population of *A. gamma* is maintained almost entirely by immigration in spring from southern Europe (Ford 1972). A particular light source in England should have a negligible influence on the breeding stock which annually

replenishes the population of *A. gamma* around it. Seasonal movement of moths over long distances is not rare (Williams et al. 1942, Williams 1958, Johnson 1969, Ford 1972) and may be sustained by wind transporting moths at altitudes sometimes hundreds of meters above most electric light sources (Glick 1965, Mikkola 1986, Raulston et al. 1986, Wolf et al. 1986).

**Failure to suppress agricultural pests and other species.** One might expect that light traps could substantially reduce or eliminate some moth populations. However, elaborate efforts to exploit such traps for pest control have failed, and successes could not be consistently replicated (Cantelo 1974, Hienton 1974). The failure has been attributed to influx of moths from outlying areas, but light trapping may fail to control insect populations even on small islands. On St. Croix, United States Virgin Islands, 250 black-light traps were deployed during a period of 43 months. The island is 208 km<sup>2</sup> in area. Although decreases in light-trap collections suggested that traps were depleting the island's sphingids (Cantelo et al. 1972a, 1972b), other studies using the same traps at the same time found similar decreases in collections of *Heliothis zea* even though traps collected only a minute fraction of the island's *H. zea* population (Cantelo et al. 1973, 1974, Snow et al. 1969). Furthermore, light-trap collections of sphingids were beginning to increase at the time the study was terminated. Meteorologic and density-dependent ecological forces may determine the size of moth populations exposed to lighting, even on isolated islands.

Failure of light traps to reduce insect populations extends beyond species of agricultural interest. Williams (1939) examined 150 species of Noctuidae and Geometridae collected in his stationary light trap during a 4-year period in Rothamsted. Comparison of numbers of individuals of each species collected from year to year provided no evidence of any consistent declines in populations, except possibly in the case of one geometrid. More recent observations at Rothamsted extended Williams' studies. Taylor et al. (1978) tabulated annual number of species and number of specimens of each trapped at Rothamsted from 1966 to 1975, and also calculated an index of diversity for each year. No downward trends are apparent, despite wide fluctuations from year to year.

**Prevalence of urban moths.** The above studies did not simulate urban conditions where lighting is dense and widespread. However, large numbers of species have been collected in urban areas in Britain and the United States (Langmaid 1959, Lutz 1941). Collections based on a nationwide network of 172 light traps in Britain suggest that moth populations in areas undergoing urban changes can substantially recover despite electric lighting (Taylor et al. 1978). In North America, some

saturniid species not only tolerate urban lighting but may actually thrive better in urban than in rural habitats. *Hyalophora cecropia* and *Samia cynthia* are two examples. The ecology of both species is complex, and numerous factors other than lighting can account for changes in their abundance in illuminated environments (Sternburg et al. 1981, Frank 1986). In New England, eight species of *Catocala* (Noctuidae) thrive in illuminated urban or suburban areas. Seven of these species can be found within a mile of downtown New Haven, and one occurs in downtown Boston. Several depend almost entirely on urban-suburban shade trees (D. F. Schweitzer pers. comm.).

**Extinctions unrelated to lighting.** Most declines and extinctions in moth populations can be linked to specific circumstances unrelated to lighting (Bretherton 1951, Ford 1972, Heath 1974). These include deforestation, agriculture, and draining of fens. Destruction of habitats as a cause of widespread declines in Lepidoptera populations has been described in detail for European butterflies (Kudrna 1986). In Britain, many species of moths became scarce around the middle of the last century, but after World War I the situation reversed, probably because of favorable climatic changes (Heath 1974). Declines in numbers of *Malacosoma americanum* (F.) (Lasiocampidae) in Winnipeg, Manitoba, have been attributed to English sparrows (*Passer domesticus* L., Passeridae) eating the moths at lamps (Krivda 1980), but *M. americanum* populations fluctuate at intervals independent of changes in lighting. Interval duration is about 10 years (Johnson & Lyon 1976). Attacks by microbial and parasitic agents probably account for periodic reductions in populations of this species (Lutz 1941).

Saturniid populations in the northeastern United States declined in the 1950's. This observation is supported by dates of last capture for species represented in regional collections, and by surveys of collectors (Ferguson 1971, Hessel 1976, D. F. Schweitzer pers. comm.). Populations of some saturniid species have since shown signs of recovery, whereas other saturniids, especially the two *Citheronia* species native to the area, have failed to recover in several states (D. F. Schweitzer pers. comm.). Declines that occurred in the 1950's coincided with widespread aerial spraying against gypsy moth, and recoveries coincided with drastic curtailment of this spraying (D. F. Schweitzer pers. comm., Gerardi & Grimm 1979). Whether pesticides can account for changes in saturniid populations is unclear. However, changes in populations of saturniids as a group correlate poorly with changes in outdoor lighting.

#### Evidence for Effects

**Small colonies exposed to lighting.** Evidence that outdoor electric lighting has the capacity to affect populations of moths is illustrated by



*Hydraecia petasitis* Doubleday (Noctuidae) in Finland. Only three or four isolated colonies are known to exist in the country. The isolation is not due to urbanization but rather to the fact that the species in Finland is at the extreme tip of its range. Two small colonies were studied, one covering 700 m<sup>2</sup>, the other 800 m<sup>2</sup>. A mark-recapture experiment conducted during 48 days in one colony demonstrated that a trap equipped with an 80-watt mercury lamp captured 53% of males in the colony and 30% of females at least once. The colony was estimated to consist of 218 individuals. These and other observations suggest that continuous light trapping could destroy this population. The authors point out that this species is only mildly attracted to light, and that the effect of light trapping might be more severe for other Lepidoptera (Väisänen & Hublin 1983). The number of moths the authors trapped probably underestimated the number that flew to the lamps (Hartstack et al. 1968).

The Finnish light-trap study demonstrates that a substantial proportion of individual moths within a geographically small colony may fly to an electric lamp. It is conceivable that disturbances in oviposition, mating, feeding, vision, navigation, dispersal, crypsis, circadian rhythms or photoperiodism would be sufficient to disrupt an already shaky population or to impede establishment of a new one. Disruptive effects would be even greater when caused by lamps in special conditions. These include lamps in traps equipped with electrocuting grids ("bug zappers") and lamps near bird feeders and bird houses. Lamps may incinerate or desiccate moths trapped inside poorly constructed or broken luminaires. Lamps near hostplants may disturb females attracted to the plants, or they may disturb males attracted to the females. Lamps in open garages and pavilions may direct moths into areas from which they cannot escape. Automobile headlamps and streetlamps divert moths into the paths of moving vehicles.

**Urbanization and fragmentation of habitats.** The same urban changes that increase outdoor electric lighting also tend to fragment habitats (MacArthur & Wilson 1967). The result is creation of small colonies exposed to electric illumination. Man has made many species of British moths in effect relict faunas, remnants of a bygone era when their habitats were much more widespread (Bretherton 1951, Ford 1972). Three species of noctuids once plentiful in southern California have been reduced to small, isolated colonies, in one instance in the vicinity of the Los Angeles International Airport (Hessel 1976). Urban gardens and parks now function as important faunal reservoirs (Frankie & Ehler 1978, Davis 1978, 1982, Owen 1978, Schaefer 1982). Urbanization increases both vulnerability and exposure of moth populations to lamps.

**Lighting as a selective force.** Outdoor lighting may act as a selective



force against particular individuals within a population. For example, it may select against individuals that tend most strongly to exhibit flight-to-light behavior. In the Finnish light-trap study, such individuals would include those that flew into traps most frequently. Industrial melanism demonstrates that urban change may cause evolutionary change in populations of moths, and that disturbances in crypsis can generate the selective forces needed to produce such evolution (Kettlewell 1973, Cook et al. 1986). Electric lighting disturbs crypsis, but also a multitude of other functions. That some species of noctuids and other nocturnal moths do not fly to nearby light sources, or do so only rarely (Bretherton 1954, Taylor & Carter 1961, Janzen 1983), suggests that evolutionary modification of flight-to-light behavior has already occurred, although the causes are unknown.

Responses to selective pressures produced by lighting may be diverse. For species active at dusk, natural selection could favor individuals that fly at the beginning of the population's flight period, rather than at the end when flight to light occurs. The evolutionary response would be a shift in flight period rather than a specific change in flight-to-light behavior. Biological clocks are in part genetically controlled, and clock mutants affecting time of eclosion and locomotor activity have been identified in *Drosophila* (Konopka & Benzer 1971, Yu et al. 1987). In moths, different races or strains of a single species exhibit different photoperiodic behavior (Gardiner 1982, Ankersmit & Adkisson 1967), and selective pressures can account for such differences (Tauber & Tauber 1978, Hoy 1978, Waldbauer 1978). On the other hand, advancing or delaying flight times could disturb species segregation mediated through allochronic flight periods (Tuttle 1985), or it could expose moths to increased predation by birds or bats that fly only at certain times. Any evolutionary response to selective pressures generated by electric lighting would have to represent a net response to opposing selective pressures.

The diversity of moth behavior around lamps suggests a multitude of possible mechanisms for reducing adverse effects of electric light. The degree to which moths of different species fly to lamps may depend on the degree to which they respond to alternative navigational cues that compete with the lamps (Janzen 1984). Suppression of flight-to-light behavior could take the form of increasing responsiveness to competing stimuli such as olfactory, geomagnetic, aerodynamic, gravitational and inertial cues, plus alternative visual cues (Baker & Kuenen 1982, Baker & Mather 1982, Schöne 1984, Janzen 1984, Riley & Reynolds 1986). Within a population of moths, variation exists not only in tendency of different individuals to fly to light, but also in tendency to linger at the light or fly past it. Variation may also exist in tendencies

to avoid lamps or oviposit near them. Evolutionary changes in response to electric lighting may be complex.

Forces opposing evolutionary reduction of flight-to-light behavior, however, are difficult to understand and assess in individual cases. Studies have employed suction traps to measure aerial densities of moth populations and at the same time light traps to measure flight to light. These studies suggest that *Xestia (Amathes) c-nigrum* (L.) (Noctuidae) is 5000 times as likely to fly to light as *Amphipyra tragopoginis* (Cl.) (Noctuidae) (Taylor & Carter 1961). Why these two noctuids behave so differently around lamps is a mystery. Failure to evolve seemingly advantageous adaptations has been well described in Lepidoptera (Ehrlich 1984). Populations of moths may resist strong selective pressures to evolve defenses against adverse effects of electric light.

**Fewer moths at urban lamps.** Evolutionary changes in wing coloration can be documented by inspection of collections of moths obtained over a period of time (Kettlewell 1973). Evolutionary changes in flight-to-light behavior cannot be documented in this way. Observations a century ago, however, are worth noting. Riley (1892: 51) advises collectors where to look for moths: "... nowadays the electric lights in all large cities furnish the best collecting places, and hundreds of species may be taken in almost any desired quantity." Denton (1900:35) was more explicit:

While employed in Washington, D.C., I made a splendid collection of the moths of that region simply by going the rounds of a number of electric lights every evening. The lamps about the Treasury Building were sometimes very productive of fine specimens and the broad stone steps and pillars were frequently littered with moths, May flies beetles, etc., where one could stand and pick out his desiderata with little difficulty. I captured several of the Regal Walnut moths (*Citheronia regalis*) and a number of our largest and handsomest sphinxes. Besides making the acquaintance of a number of insects new to me, I met several entomologists who, like myself, had been attracted to the lights by the abundance of specimens.

Today lamps in big cities such as Washington, D.C., Philadelphia, and Boston rank among the worst places to collect moths or meet entomologists. Reductions in numbers of moths flying to lamps have been noted in other locations (Hessel 1976, Muller 1979, Janzen 1983). Decreases in moths at urban lamps can be explained by many factors, including declines in moth populations, dilution of moths among thousands of city light sources, and suppression of flight-to-light behavior as a result of diffuse background light. However, reductions in numbers of moths flying to urban lamps are what one would expect if urban moths today were genetically less inclined to fly to lamps than were those a century ago.

In densely illuminated urban environments, lighting may have favored species that either fly during the day, do not fly to lamps, or do

not fly at all. Urban pests exemplify such species. These include sesiids (Engelhardt 1946) and domestic tineids (Ebeling 1978). Species with flightless females include the bagworm moth, *Thyridopteryx ephemeraeformis* (Haw.) (Psychidae), gypsy moth, *Lymantria dispar* (L.), (Lymantriidae), white-marked tussock moth, *Orgyia leucostigma* (J. E. Smith) (Lymantriidae), and fall cankerworm, *Alsophila pometaria* (Harris) (Geometridae) (Lutz 1941, Drooz 1985). The two urban saturniids, *Hyalophora cecropia* and *Samia cynthia*, do not commonly fly to urban light sources (G. P. Waldbauer pers. comm., Covell 1984). The extent to which lighting may have influenced the kinds of moths inhabiting densely illuminated urban environments is unclear.

#### METHODS TO REDUCE DISTURBANCES

Low-pressure sodium lamps may be used to reduce disturbances caused by lighting. Low-pressure sodium lamps elicit flight-to-light behavior less frequently than do other lamps (Robinson 1952). They do not disturb certain circadian rhythms of Lepidoptera and other insects (Frank & Zimmerman 1969, Bruce & Minis 1969, Pittendrigh et al. 1970, Truman 1976). The low-pressure sodium lamp radiates less energy than does any other kind of lamp of equal illuminance (Finch 1978).

A variety of measures may protect moths from adverse effects of outdoor lighting. Lamp-free reserves such as sheltered hollows shielded from lighting have been suggested to save the glow worm, *Lampyrus noctiluca* L. (Coleoptera: Lampyridae), a species whose survival in Britain may be threatened by outdoor lighting (Crowson 1981). To reduce lighting impact in habitats already exposed to lamps, the most effective action is to turn off the lamps. Low-pressure sodium lamps may replace other lamps when illumination is essential. Filters to block ultraviolet light may be installed over mercury vapor lamps, and shields may be placed around lamps to block stray light. Low-watt orange-colored incandescent lamps ("bug lights") may replace ordinary incandescent lamps, but some moths fly to these lamps. Bird feeders may be removed from windowsills, lampposts, and other sites close to light sources. "Bug zappers" should be turned off. Natural light-traps such as open garages may be closed to prevent entry of insects. Operators of nearby commercial light sources such as illuminated billboards may be contacted and invited to save money and moths by turning lamps off during those hours of night and early morning when billboards are rarely seen.

Although the feasibility of such changes may be questioned, several North American cities have taken similar steps to reduce light pollution. Light pollution interferes with astronomical work at observatories (Hen-

dry 1984). These cities have converted streetlamps to low-pressure sodium, required ultraviolet-blocking filters over mercury lamps, imposed curfews on the use of commercial lighting, and mandated shielding of luminaires (Hendry 1984). Low-pressure sodium lighting, however, has provoked political controversy on aesthetic and other grounds (San Jose Committee of the Whole 1980).

### CONCLUSION

Effects of outdoor lighting may be divergent. They vary according to species, lamps, and habitats. Improved levels of illumination may increase nocturnal vision, but creation of visual artifacts may disturb vision. Increased numbers of lamps may promote flight-to-light behavior, but high levels of background light may suppress this behavior. Expansion of streetlighting may increase flight to streetlamps, but shifts from mercury to sodium lamps may decrease it. Diversion of moths to lamps may increase numbers of moths in illuminated areas, but diversion of moths away from lamps may decrease numbers. Lamps may suppress oviposition in the laboratory, but oviposition may increase or decrease near lamps in the field. Clumping of moths near lamps may increase predation by birds and bats, but destruction of parasitic wasps and flies at lamps may decrease predation. Disturbances such as habitat destruction and urbanization may further confound effects of outdoor lighting.

Several conclusions emerge from the observations on lighting. Outdoor lighting may destroy vast numbers of individual moths without apparently suppressing populations of moths. However, it disturbs some populations more than others, and it disturbs some individuals more than others in the same population. It generates selective pressures favoring adaptations for protection against adverse effects of lamps. The result may be evolutionary changes in behavior, or changes in the kinds of moths inhabiting illuminated environments. These changes may increase through time as urban expansion fragments habitats and exposes smaller moth populations to electric illumination.

Conservation efforts need to consider adverse effects of outdoor lighting. If one wishes to protect Lepidoptera in small, endangered habitats exposed to outdoor lighting, reducing or changing exposure may be helpful. In such habitats light traps including "bug zappers" may deplete populations of moths. Some cities have attempted to reduce light pollution to protect astronomical observatories. Whether similar large-scale restrictions on lighting might help to conserve Lepidoptera has yet to be demonstrated.

Future research could help clarify lighting impact. Despite abundant evidence that outdoor lighting affects individual moths, few studies

have attempted to quantify lighting effects on moth populations. Evidence that lighting has suppressed populations of particular moths such as saturniids is weak. Studies similar to those on the effects of illumination of orchards and cotton fields (Herms 1929, 1932, Nomura 1969, Nemec 1969) could be extended to other settings and species. Faunal surveys, life history studies, and ecological studies could examine Lepidoptera in differently illuminated environments. Behavioral and physiological studies could investigate the possible evolution of tolerance to adverse effects of lighting. The method might include comparison of Lepidoptera sampled from large geographic regions that possess different levels or kinds of outdoor illumination.

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## HYBRIDIZATION BETWEEN TWO SPECIES OF SWALLOWTAILS, MEIOSIS MECHANISM, AND THE GENESIS OF GYNANDROMORPHS

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**ABSTRACT.** Hybridization between *Papilio machaon* L. and *P. polyxenes asterius* Stoll was carried out over four generations by backcrossing black female  $F_1$  and further hybrids with wild *machaon* males. A bilateral gynandromorph (symmetrical mosaic for the black-yellow phenotype) was obtained. In the fourth generation, one brood from a single female had negligible mortality but yielded an abnormal sex ratio opposite that predicted by Haldane's Rule (45 males/86 females, ca. 1:2). The black-yellow character followed a perfect 1:1 segregation. Reexamination of previous data suggests that meiosis in Lepidoptera follows an unusual pattern: the sister chromatids segregate during the first division, and crossing over is frequently absent in females. Bilateral gynandromorphs are generally due to fertilization of binucleate oocytes. Segregation during the first meiotic division also can explain the patterns of gynandromorphs arising as autosomal mosaics, such as those described here.

**Additional key words:** *Papilio machaon*, *P. polyxenes asterius*, Papilionidae, sex ratio.

Hybridization between *Papilio machaon* L. from Europe and Japan and *P. polyxenes asterius* Stoll from the United States was first undertaken more than 20 years ago (Clarke & Sheppard 1953, 1955, Ae 1966). Commercial availability of pupae of both species has allowed many breeders to easily carry out this cross since then. We recently performed such crosses, and our results are peculiar. Moreover, a spectacular gynandromorph emerged from one of our broods, and we compare this specimen with other examples recently described by Clarke and Clarke (1983).

### MATERIALS AND METHODS

*Papilio polyxenes asterius* stocks were established from diapausing pupae obtained from Chicago, Cook Co., Illinois, and we obtained *P. machaon* from Cahors, Lot, France. The insects were hand-paired using the technique of Clarke (1952). Mated females were fed with a honey-water mixture (1:10), and allowed to oviposit in a gauze cage on carrot (*Daucus*) leaves. Either sunshine or light of a 60 W bulb at a distance of 20 cm was used to activate the insect. Number of ova laid per female

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was between 50 and 100, sometimes more. Larvae were reared on carrot leaves, or occasionally on other Umbelliferae. While no pathology was noticed in former broods, it has inhibited breeding in recent years. This fact may be related to extensive use in our neighborhood of the insecticide "Bactospéine", which contains strains of *Bacillus thuringiensis* Berl. Many diseased pupae and adults showed teratological atrophies comparable to those induced by toxin of this bacterium (Burgerjon & Biache 1967). Similar abnormalities also have been observed in pure strains of *Papilio polyxenes asterius* bred in the United States (Carter & Feeny 1985).

We encountered difficulties obtaining functional males in our breeding stocks, even among non-hybrids. Thus, hybrid females were always used, while the males were pure *machaon* from wild stocks. Crosses were performed over four generations.

### RESULTS

Several broods comprised the  $F_1$  generation ( $\text{♀ } asterius \times \text{♂ } machaon$ ), and gave the same results as those of Clarke and Sheppard's (1953, 1956) experiments: each offspring was as melanic as *asterius* and the anal eye-spot was intermediate.  $F_2$  backcrosses ( $\text{♀ } F_1 \times \text{♂ } machaon$ ) gave the expected 1:1 segregation between "black" and "yellow". In one brood, a remarkable gynandromorph was obtained (Figs. 1, 2). It is bilateral, with all of the left side being female with a "black" phenotype, and the eye-spot very close to *machaon*. The underside, although melanic, shows a strong *machaon* influence in distal parts of the wing. These features are characteristic of this kind of backcross. Markedly smaller, the right side is mainly male, and extremely *machaon*-like. However, on the hindwing, a melanic patch is present in the anal part. Its shape is complex, and its anterior border coincides with a compartment limit (Sibatani 1983) in the middle of the cell. The body is conspicuously halved in "black" and "yellow".

The third and fourth generations were obtained by pairing melanic females from the previous backcross with wild male *machaon*. As noted by Clarke and Sheppard (1956), fertility gradually increased. In the fourth generation, we were fortunate to obtain a large, healthy brood from a single female: 131 adults from 135 ova. Among them, 65 were of the "yellow" phenotype (18 males, 48 females) and 66 of the "black" (27 males, 38 females). Therefore, if the "yellow"/"black" ratio of 65/66 is truly 1:1, the sex ratio is strongly distorted (45/86,  $\chi^2 = 12.83$ ,  $P < 0.001$ ). The latter proportion is close to a 1:2 ratio. The cross presents another intriguing feature: the excess of females is more marked in the "yellow" phenotype than in the "black", where it does not even reach a significant level (27/38,  $\chi^2 = 1.86$ ,  $P < 0.2$ ). Analysis of these data





FIGS. 1, 2. *P. machaon* × *P. polyxenes asterias* F<sub>2</sub> hybrid, bipartite mosaic and gynandromorph. 1, Dorsal surface; 2, Ventral surface. Shown at ⅔ natural size.

through a contingency table indicates that this abnormality of distribution is on the borderline of significance ( $\chi^2 = 2.955$ ,  $0.10 > P > 0.05$ ).

A second gynandromorph arose in another brood of the fourth generation; it is a "mosaic", with the same "black" phenotype throughout. Gynandromorphism is apparent only in the parts where the male differs from the female. This specimen resembles closely those described by Clarke et al. (1977). No element of symmetry could be observed in this individual.

### DISCUSSION

Some gynandromorphs of *Papilio* have already been described. A discussion once arose in the *News of the Lepidopterists' Society* about interpretation of gynandromorphs of *Papilio glaucus* L. (Walsten 1977, Silberglied 1977); a reanalysis of these examples was provided by Clarke and Clarke (1983). We next review some problems raised by sex genetics and the origin of gynandromorphs in Lepidoptera.

Morgan and Bridges (1919) showed that, in *Drosophila*, gynandromorphism is due to an irregular disjunction of sex chromosomes, leading to the loss of an "X" in one of the daughter cells. So, one-half of the organism would bear an "XX" set and would be female, and the other an "XO" and would be male (the Y chromosome is considered to bear very little information in this insect). In only one case in Lepidoptera has this mechanism been conclusively demonstrated, in the moth *Abraxas grossulariata* (Morgan & Bridges 1919), but Clarke and Clarke (1983) consider it a very likely explanation in some other cases. In most other examples, another mechanism seems to be involved: fertilization of a binucleate oocyte, as explained by Goldschmidt (1931). During meiosis,

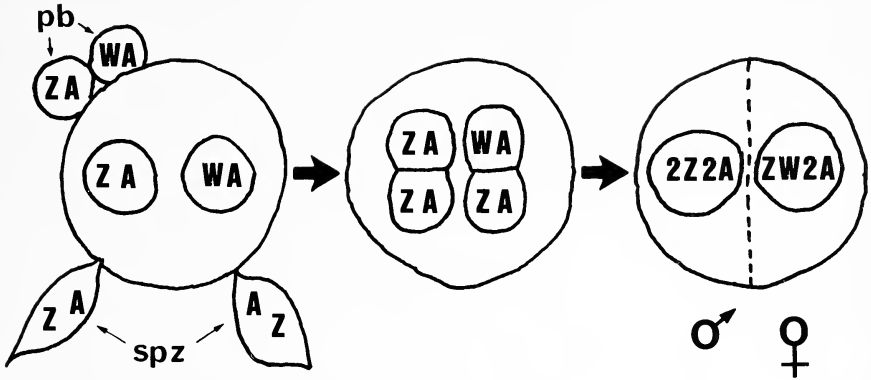


FIG. 3. Schematic presentation of the mechanism producing gynandromorphs from a binucleate oocyte. Z, W: sex chromosomes; A: autosomal stock. pb: polar bodies from the former division; spz: the two spermatozoa which will fertilize both female pronuclei.

the two successive divisions lead to four haploid nuclei. Normally, three of them are eliminated. In some cases, which appear to be scarce, but whose frequency may be increased by certain mutations, two nuclei remain in the central zone of the oocyte, and both become fertilized. There follows a juxtaposition of the two eggs, which may have a genetic composition as different as any combination of two brothers and sisters. Figure 3 illustrates this phenomenon; we use "Z" and "W" for heterochromosomes, ZZ being male and ZW female. This phenomenon has been observed and photographed by Goldschmidt and Katsuki (1927).

As Robinson (1971) pointed out, this mechanism raises problems related to chromosome segregation in meiosis. Meiosis may proceed in two ways:

- 1) Sister chromatids issuing from the same single parental one may separate in the first mitosis of meiosis; the second mitosis therefore dissociates mother- and father-issuing homologous chromosomes.
- 2) The first mitosis separates mother- and father-issuing sets of chromosomes, and the second one, the sister chromatids.

The second way is considered normal in animals and plants. Of course, division of the centromere is expected to play a key role in this phenomenon. Actually, it is very difficult to observe the process cytologically and to demonstrate it genetically. It is only in oocytes that daughter cells undergo such a dissimilar fate.

The study of gynandromorphs and mosaics originating from binucleate oocytes may provide a clue to the precise order of chromatid segregation. When such abnormalities arise, they are most likely due to the two pronuclei issuing from the second mitosis remaining in the

middle of the oocyte. Gynandromorphs and bipartite mosaics can arise only if chromosome sets present in each symmetrical fertile pronuclei are genetically different. This implies that meiosis follows the first way above.

Cockayne (1935) clearly showed that there are two types of respective segregation in autosomes and sex chromosomes. 1) In *Bombyx mori*, gynandromorphs and uni- or bisexual mosaics are observed with the same frequency (Goldschmidt & Katsuki 1927). This shows that the two fertile pronuclei may either be both "Z" or both "W", or one "Z" and one "W", and it means that the chromosomes are segregating at random, likely due to an achiasmatic meiosis. 2) In *Argynnis paphia*, Goldschmidt and Fischer (1927) studied a strain where gynandromorphism occurred regularly, probably because of a mutation producing abnormal meiosis. In some cases, the autosomal and sex-conditioned mutant "*valesina*" was involved in the crosses. In contrast with *Bombyx*, "*valesina*"-normal mosaics are only observed when there is also gynandromorphism, and no unisexual mosaic occurs in this strain. The unambiguous conclusion (not stated by Goldschmidt and Fischer or Cockayne) is that always, when a binucleate oocyte is formed, one pronucleus bears a "Z" and the other a "W"—a strong argument in favor of meiosis with preliminary separation of sister chromatids. In the sphingid *Laothoe populi*, and in many other instances, things appear identical. An illustrative example was recently provided by Platt (1983), in artificial hybrids of *Limenitis arthemis* and *L. lorquini*; he also interpreted the bipartite mosaic-gynandromorph he obtained by the "double egg" theory. However, we are reminded of a halved "*alba*"-orange female of *Colias croceus* figured by Frohawk (1938); since various kinds of gynandromorphs have been described in this species (including "*alba*" female-orange male), this case might rather correspond to the silkworm type; however, mosaics may arise from various causes and, isolated, this record remains inconclusive.

Previous paragraphs deal only with bipartite gynandromorphs and mosaics; however, most sexual mosaics are asymmetrical, which can be explained in two ways: either, in the case of binucleate oocytes, one pronucleus becomes shifted from the central region of the oocyte, or sex chromosomes segregate abnormally during further division of embryonic cells. This latter event most likely explains the minute patches which characterize the bulk of so-called gynandromorphs.

The first gynandromorph described in this study fits perfectly with the double-oocyte theory, and supports the assumption that meiosis obeys the first-named way in *Papilio*. In the double oocyte that gave rise to this individual, the left pronucleus was "W" and "black" and the right one "Z" and "yellow" (Fig. 4). The only puzzling point comes

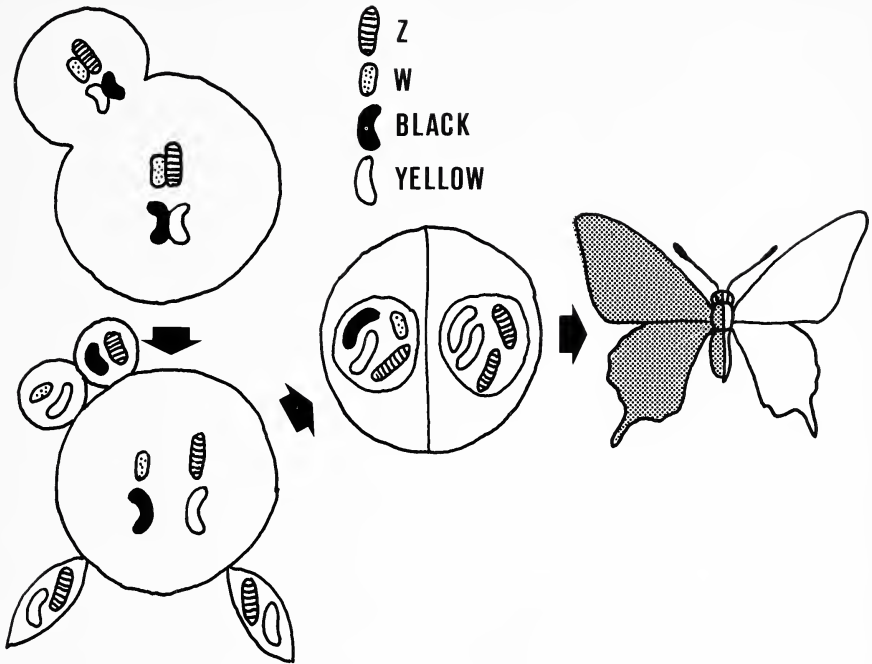


FIG. 4. Scheme of the mechanism leading to the gynandromorph of Figs. 1, 2. Only the color character-bearing autosome pair is figured.

from the small melanic patch on the right hindwing. It is inadmissible that it arose from a chromosome loss, since “black” is dominant and could not be present in the genetic stock of the right half. Thus it should be due either to presence of an uneliminated third pronucleus, remnant from the first division of meiosis, or to an erratic cell coming from the left half. The second gynandromorph may be best explained by an atypical segregation of sex chromosomes during embryogenesis. If it arose from a binucleate oocyte, this would imply that achiasmatic meiosis could occur in *Papilio* as in *Bombyx*.

According to Suomalainen (1965), the first-named type of meiosis is determined by the holocentric nature of centromeres, which he has indeed observed in Lepidoptera; he states also that, in this order, no crossing over occurs in the female sex. These assumptions have suffered controversy from Robinson (1971) and White (1973) as remaining undemonstrated in the whole of Lepidoptera, but they have been firmly ascertained for some species, such as *Bombyx mori* (Tazima 1964), *Heliconius* (Turner & Sheppard 1975), *Anagasta kuehniella* (Traut 1977).

The abnormal sex ratio observed in one brood of the fourth generation

(which is corroborated by other less quantitative observations made at the same time) is most difficult to interpret. We have no definitive explanation to propose; we only offer remarks that may help future investigations. The distortion goes against Haldane's (1922) Rule. Here, it is the heterogametic sex that is favored; the  $\delta/\text{♀}$  ratio is close to 1:2. It is not possible to explain this discrepancy by the death of one-half of the males, since the mortality from egg to adult was very low. We must invoke a possible abnormality during meiosis.

A non-disjunction of "Z" chromosomes during oogenesis could produce a sex ratio distortion in the direction observed. It should give rise to a proportion of 2 (W, A) oocytes, 1 (ZZ, A) and 1 (O, A). Hence, following fertilization, we should have 1/2 ZW, 2A normal females, 1/4 ZO, 2A females (such a formula is usually considered to correspond to females) and 1/4 ZZZ, 2A males. But should the two latter types of individuals display a viable phenotype? We could not detect any abnormality in offspring of the concerned brood. Moreover, if generalized, this mechanism should give rise to 3/4 females, while we observed 45/86 ( $\chi^2 = 6.5$ ,  $P < 0.01$ ); therefore, non-segregation acted only partially.

Meiotic drive is another phenomenon which could lead to sex ratio distortion. This is a preferential segregation of certain chromosomes in functional gametes (detailed review in Zimmering et al. 1970). Recent data indicate that this phenomenon is rather widespread, and involves a higher frequency sex and "B" (heterochromatine) chromosomes. Sex chromosomes differ in both of our species by a heterochromatic segment present only in *machaon*. Moreover, the "W" from *asterius* does not pair perfectly with the "Z" from either species (Clarke et al. 1977). Do these peculiarities trigger meiotic drive preferentially directing the "Z" towards a polar body? Such a phenomenon would produce normal karyotypes; being unaware of the problem, we did not check karyotypes.

Moreover, we should consider that sex ratio distortion perhaps affects the "yellow" phenotype somewhat more; this could mean that there is "attraction" between the *asterius*-originated "W" and the color-controlling autosome which comes from *machaon*. One possible explanation is that these two chromosomes possess certain sequences in common, and that they could pair, at least partly, during meiotic prophase. This should obviously affect further segregation, the color-bearing autosomes being the "drivers", as is indicated by their overall 1:1 proportion. Both species should therefore differ by a translocation between sex chromosomes and color-bearing autosomes. This hypothesis is not as fancy as it may appear at first sight, since in related American species such as *Papilio glaucus*, the color-controlling segment itself is carried on the "W" chromosome (Clarke & Clarke 1983).



## CONCLUSION

Reexamination of previous data and analysis of the experiments presented here allow us to conclude that:

1) In butterflies, at least in the vast majority, meiosis obeys a rather unusual pattern where chromatid segregation follows an order opposite the normal one. This is also probably true for moths (the Silkworm case being the most extreme, since in its meiosis it is achiasmatic).

2) Bilateral gynandromorphs arise most often from fertilization of a double oocyte. The determinism of mosaic gynandromorphs is more complex and may result from completely different causes.

3) In *Papilio*, one can carry interspecific crosses over a large number of generations by using backcrosses, in a kind of "monitored introgression".

4) Even in *Papilio*, however, a residual amount of genetic incompatibility occurs. Sex chromosomes are the most sensitive to disturbances resulting from this incompatibility.

We surmise that some kind of abnormal chromosome segregation takes place in interspecific crosses, and we hope our findings will stimulate further research on these questions.

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## EXTERNAL GENITALIC MORPHOLOGY AND COPULATORY MECHANISM OF *CYANOTRICHA NECYRIA* (FELDER) (DIOPTIDAE)

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**ABSTRACT.** External genitalia of *Cyanotricha necyria* (Felder) exhibit characters that occur in the Notodontidae and Dioptidae. These provide further evidence that the two groups are closely related. Dissection of two *C. necyria* pairs *in copulo* revealed two features unique among copulatory mechanisms described in Lepidoptera. First, only the male vesica, rather than the aedoeagus and vesica, are inserted into the female. Secondly, during copulation the female is pulled into the male abdomen, and his eighth segment applies dorsoventral pressure on the female's seventh abdominal segment. This mechanism is facilitated by a long membrane between the male eighth and ninth abdominal segments. The first trait is probably restricted to only some dioptid species, while the second may represent a synapomorphy for a larger group that would include all dioptids, and all or some notodontids.

**Additional key words:** Noctuoidea, Notodontidae, Josiinae, functional morphology.

Genitalic structure has been one of the most important sources of character information in Lepidoptera systematics. Taxonomists often use differences in genitalic morphology to separate species, and homologous similarities have provided characters for defining higher categories in Lepidoptera classification (Mehta 1933, Mutuura 1972, Dugdale 1974, Common 1975). Unfortunately, we know little concerning functional morphology of genitalia. A knowledge of function may aid in determining homology of genitalic structures, something that has proved to be extremely difficult and controversial. In addition, a functional approach can provide important new characters for understanding phylogenetic relations. For example, Stekolnikov and Kuznetsov (1982) used functional morphology of male genitalia to provide characters for higher classification of ennomine geometrids, and Stekolnikov (1967a) contributed new data concerning familial relations among butterflies. In this paper I describe the external genitalia and mechanism of copulation in a dioptid moth, *Cyanotricha necyria* (Felder).

Forbes (1939) was among the first to examine musculature of male genitalia in Lepidoptera, and his study provided the basis for subsequent research (Birket-Smith 1974). Several workers have described musculature of male and female butterfly genitalia (Shirozu & Yamamoto 1953, Hannemann 1954a, 1954b; Ehrlich & Davidson 1961, Stekolnikov 1967a), while there have been fewer such studies on moths (Hannemann 1957, Stekolnikov 1967b).

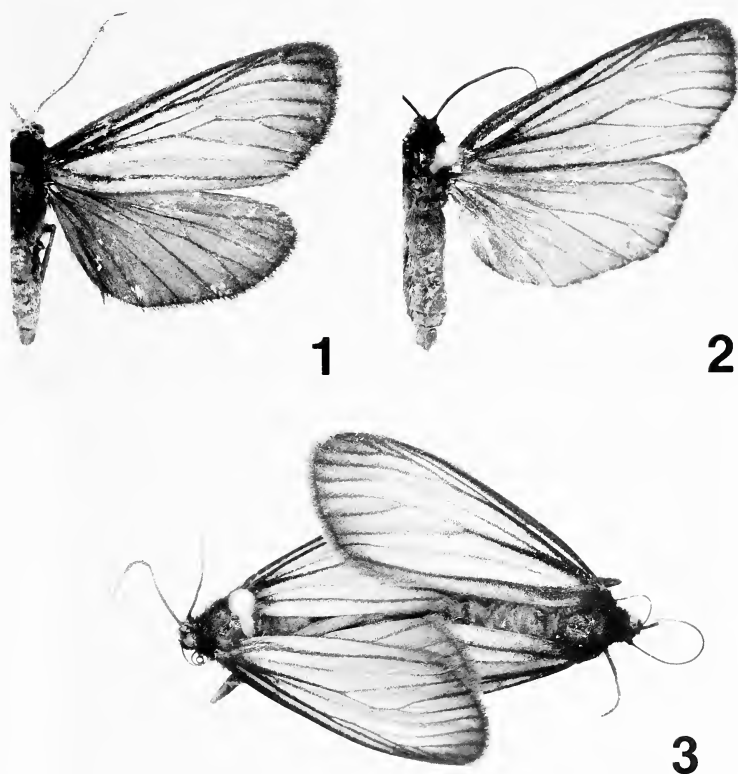
Studies of copulatory mechanisms in Lepidoptera are rare. Perhaps

the first was that of Chapman (1916a, 1916b), who attempted to determine the mechanism of copulation in lycaenids. However, he was unable to adequately preserve specimens *in copulo*. Arnold and Fischer (1977) analyzed genitalic muscle attachments and the method of copulation in three *Speyeria* species (Nymphalidae), and De Jong (1978) described the copulatory mechanism in *Carcharodus boeticus* Reverdin (Hesperiidae). Stekolnikov (1965) compared copulatory mechanisms of four moth species, *Spilosoma menthastri* Esper (Arctiidae), *Acrionicta rumicis* L. (Noctuidae), *Antheraea pernyi* Guérin (Saturniidae), and *Dendrolimus pini* L. (Lasiocampidae). In a remarkable series of papers, Callahan (1958, 1960), Callahan and Chapin (1960), and Callahan and Cascio (1963) presented a detailed analysis of copulation, spermatophore production, and egg formation in Noctuidae. They examined 11 noctuid species, including *Helicoverpa zea* (Boddie), *Pseudaletia unipuncta* (Haworth), *Peridroma saucia* (Hübner), and 8 members of Plusiinae. Their methods included serial dissection of moth pairs at various stages during copulation.

The study described here is the first on moths related to notodontids, and illustrates some unique features concerning their genitalia and mechanism of copulation. *Cyanotricha necyria* is a member of Diopitidae, a group comprising approximately 400 species of diurnal, Neotropical moths (Bryk 1930, Hering 1925). Although it is acknowledged that they are closely related to Notodontidae (Franclemont 1970), their precise phylogenetic position remains unresolved; the group may ultimately be reclassified as a notodontid tribe (Minet 1983, Miller 1987, S. Weller unpubl.). The genus *Cyanotricha* Prout, which contains only two species, *C. necyria* and *C. bellona* (Druce), was placed by Kiriakoff (1950) in the diopitid subfamily Josiinae, a well-defined monophyletic group of approximately 100 species (J. Miller unpubl.). *Cyanotricha necyria* (Figs. 1 & 2) is an iridescent blue-green moth with an orange-brown dash at the forewing base between veins Sc and Rs, and a forewing length between 15 and 18 mm. It is found from central Peru N to southern Colombia, whereas the other *Cyanotricha* species, *C. bellona*, which is less common in museum collections, has been recorded only in central Peru at elevations up to 4200 m. Like many other members of Josiinae, *C. necyria* larvae feed on *Passiflora* (Passifloraceae), and the moth is currently being tested as an agent to control the spread of *P. mollissima* (HBK) Bailey, a forest weed in Hawaii (Markin et al. in press).

#### METHODS

Two pairs of pinned *Cyanotricha necyria*, preserved *in copulo*, were found in the collection at the United States National Museum. Each



FIGS. 1-3. *Cyanotricha necyria* (Felder) in dorsal view. 1, Male; 2, Female; 3, *In copulo*, male at left.

had been prepared by putting a pin through the male thorax, and the wings of the male and female had been left folded (Fig. 3). According to label data, both pairs were from the Dognin collection and had been collected in the "Environs de Loja", Ecuador, by Abbé Gaujon, one pair in 1885 and the other in 1886.

For both pairs I used the same dissecting technique. The abdomens were broken from the male and female thoraces and placed, still joined, in 10% KOH for 12 h. They were then moved to 70% ethanol, cleaned of scales and soft tissues, and drawn using a camera lucida attached to a dissecting microscope. Drawings were made at two points during dissection: (1) with abdominal segments 1-6 of the male and female removed; and (2) with abdominal segments 7 and 8 and the left valve



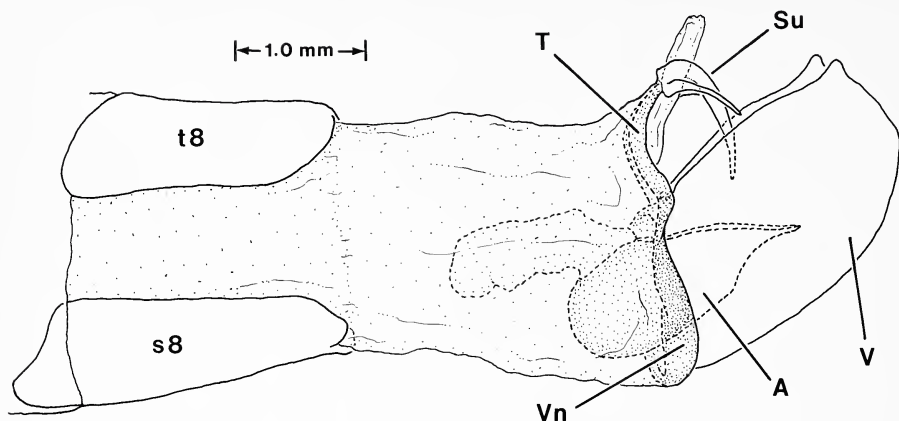


FIG. 4. Male terminalia of *C. necyria* in lateral view, anterior at left. A, aedeagus; s8, sternite 8; Su, uncus; T, tegumen; t8, tergite 8; V, valve; Vn, vinculum.

of the male removed, and abdominal segment 7 of the female removed. These drawings were overlaid to produce Fig. 11.

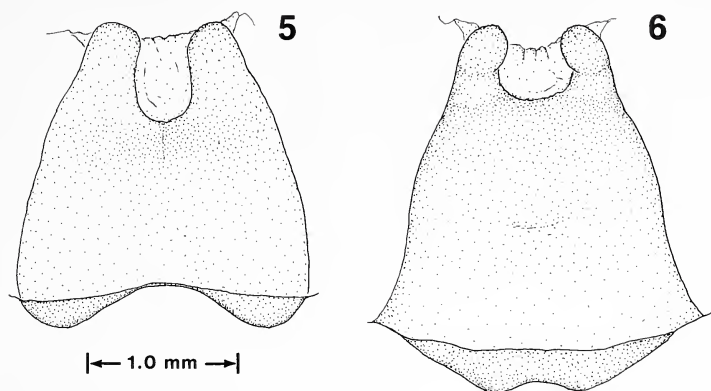
To better understand genitalic morphology in *C. necyria*, I dissected three additional males and three additional females, all from the same locality and collector as the pairs taken *in copulo*. The unpaired specimens were prepared and stained using techniques previously described (Miller 1987). All preparations are in the U.S. National Museum, Washington, D.C.

Morphological terminology follows Klots (1970), Sibatani (1972), and Ogata et al. (1957). Rather than follow the recommendation of Ogata et al. and Sibatani, who proposed the term *sociuncus*, I use two terms, *socii* and *uncus*, following Klots.

## RESULTS AND DISCUSSION

### General Features of *Cyanotricha necyria* Genitalia

External genitalia of *C. necyria* exhibit features unique to notodontids and diopitids. These strengthen the argument that the two groups are closely related. In *C. necyria* there is a long membrane between segment 8 and the tegumen + vinculum (Fig. 4). The latter are collectively termed the ring, which is thought to be homologous with abdominal segment 9 (Snodgrass 1935, Klots 1970). Genitalia in this species are normally enveloped within the abdomen. In *Speyeria*, where there is also extrusion of male genitalia during mating, movement is effected by protractor and retractor muscles, aided by hemolymph pressure (Arnold & Fischer 1977). An extremely long membrane between segments 8 and 9, combined with ability to withdraw genitalia inside the



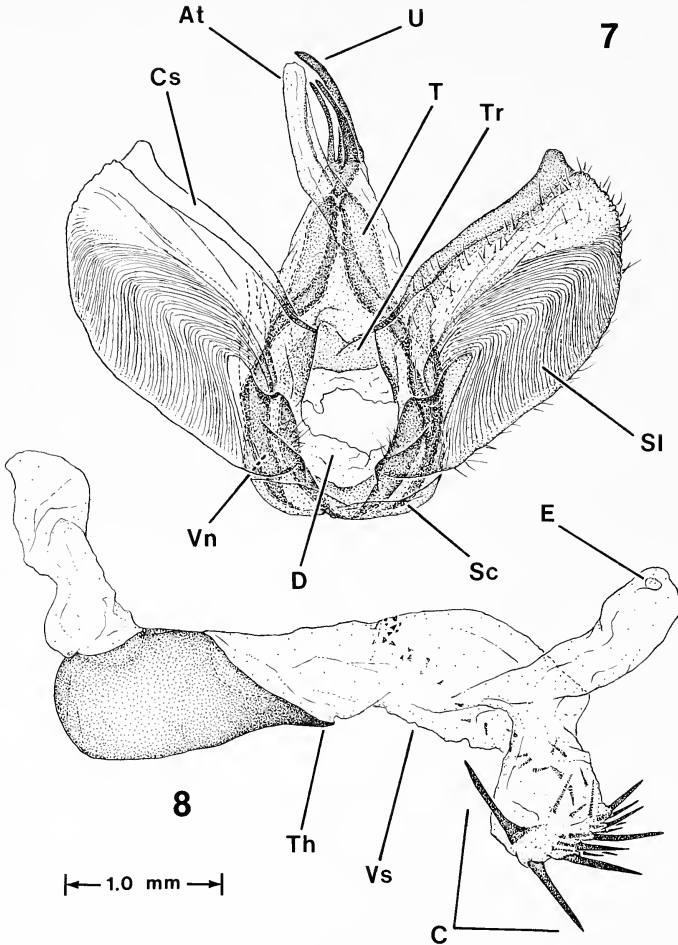
FIGS. 5, 6. Male eighth abdominal segment of *C. nectomyria*. 5, Tergite (dorsal view); 6, Sternite (ventral view).

abdomen, is typical of dioptids, but is also found throughout Notodontidae (Mehta 1933). This trait may represent a synapomorphy for the notodontid-related groups.

The male eighth abdominal segment in dioptids and notodontids is usually modified. In *C. nectomyria* there are excavations along the posterior margins of the tergite and sternite, and apodemes on their anterior margins (Figs. 5 & 6). In many dioptids and notodontids the posterior margin of the sternite and tergite is heavily sclerotized, sometimes bearing spines (J. Miller unpubl.). There is also much variation in shape of the apodemes on the anterior margin of sternite 8; they are frequently much longer than in *C. nectomyria*.

The sacculus of the valve in *C. nectomyria* is large with numerous pleats (Fig. 7), and the rest of the valve, except for the costa, is membranous. The pleated sacculus was described by Barth (1955) for *Hemiceras* (Notodontidae), but is another feature found frequently in dioptids and notodontids (Forbes 1942, Holloway 1983, Miller 1987). The pleats enclose androconia, and probably unfold during courtship, extruding the scales, which then presumably disseminate male scent. Mehta (1933) characterized notodontids as lacking the saccus, an internal extension of the vinculum. Male genitalia of *C. nectomyria* illustrate that the saccus is absent in some dioptids as well. The slender uncus and socii are hinged on the tegumen.

The aedoeagus of *C. nectomyria* (Fig. 8) is typical in shape for members of Josiinae, being short, deep dorsoventrally, and large relative to the rest of the genitalia. A row of cornuti on the vesica, terminating in a set of robust, spinelike cornuti, is also common in the group (J. Miller unpubl.).



FIGS. 7, 8. Male genitalia of *C. necyria*. 7, Genitalia in posterior view with aedoeagus removed; 8, Aedoeagus in lateral view (anterior at left). At, anal tube; C, cornuti; Cs, costa of valve; D, diaphragma; E, opening of vesica; Sc, saccus; Sl, sacculus; U, uncus; T, tegumen; Th, ventral tooth of aedoeagus; Tr, transtilla; Vn, vinculum; Vs, vesica.

In female genitalia of *C. necyria* (Fig. 9), tergite 8 is membranous dorsally. The ostium is surrounded by postvaginal and antevaginal plates, which hinge on a point dorsal to the opening. There are small spines inside the proximal portion of the corpus bursae. A feature found in *C. necyria* and only a few other dioptrids is the large, convoluted, sclerotized band which wraps around the corpus bursae. In noctuids, large muscles attach to the corpus (Callahan & Cascio 1963). Once the male has deposited the spermatophore in the corpus bursae, these mus-

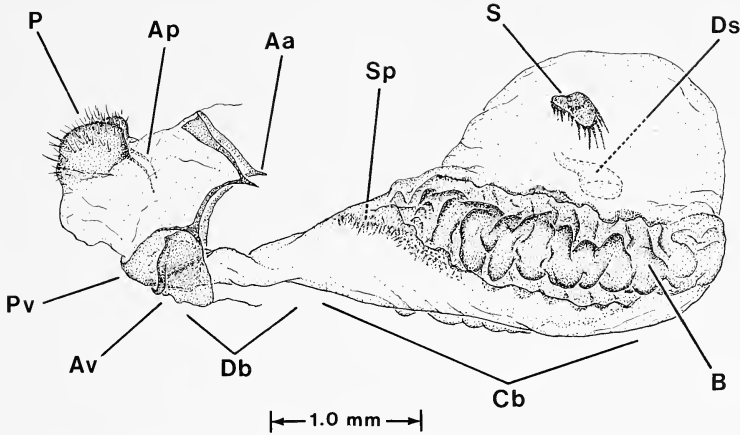
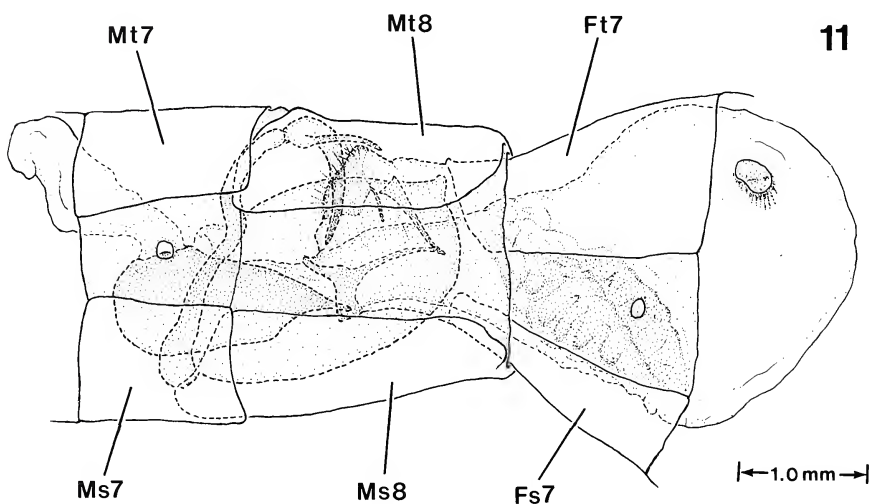
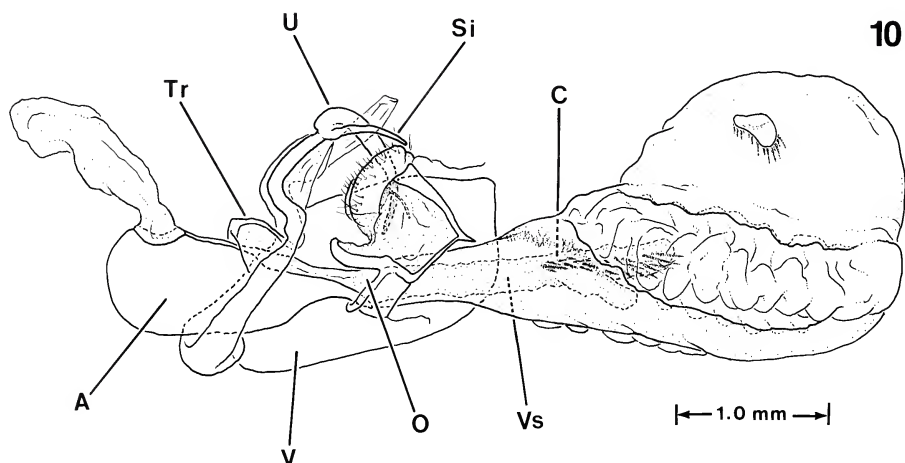


FIG. 9. Female genitalia of *C. necyria* in lateral view, anterior at right. Aa, anterior apophyses; Ap, posterior apophyses; Av, antevaginal plate; B, sclerotized band; Cb, corpus bursae; Db, ductus bursae; Ds, ductus seminalis; P, papillae anales; Pv, postvaginal plate; S, signum; Sp, basal spines of corpus bursae.

cles are thought to squeeze seminal fluid and sperm into the ductus seminalis. The sclerotized band of *C. necyria*, in conjunction with these muscles, may serve to break up the spermatophore. In *C. necyria* the ductus seminalis is located laterally on the corpus bursae, whereas in most dioptids it is located on the ductus bursae (J. Miller unpubl.). The signum is composed of a group of long spines protruding into the corpus bursae from a concave sclerotized region. Petersen (1907) and Callahan (1958) suggested that the signum functions to hold the spermatophore in place. It is a site of muscle attachment in *Helicoverpa zea* (Callahan & Cascio 1963).

#### Copulatory Mechanism of *Cyanotricha necyria*

The interrelations of male and female genitalia during copulation are shown in Figs. 10 and 11. Between the papillae anales of the female, a membranous invagination allows for insertion of the male uncus, which is reflexed downward. In these preparations the uncus almost engages the postvaginal plate of the female. In freshly preserved material with the musculature intact, it most likely would do so. Stekolnikov (1965) found that the uncus engages the postvaginal plate in *Spilosoma menthastri*; the configuration he described is almost identical with that of *C. necyria*. Stekolnikov stated that the uncus in *Acrionicta rumicis* engages the female's eighth sternite, but his illustration suggests that the 'eighth sternite' in *A. rumicis* is the same structure as the postvaginal plate in *Spilosoma* and *Cyanotricha*.



FIGS. 10, 11. Lateral view of male and female *C. necyria* in copulo, anterior of male at left, anterior of female at right. **10**, Pair #1 with abdominal segments 1-8 and left valve of male removed, and abdominal segments 1-7 of female removed; **11**, Pair #2 with abdominal segments 1-6 and left valve of male removed, and abdominal segments 1-6 of female removed. A, aedoeagus; C, cornuti; Fs7, female sternite 7; Ft7, female tergite 7; Ms7, male sternite 7; Ms8, male sternite 8; Mt7, male tergite 7; Mt8, male tergite 8; O, ostium bursae of female; Si, socii; Tr, transtilla; U, uncus; V, valve; Vs, vesica.



In *C. necyria* the socii rest on top of the papillae anales during copulation and would seem to apply downward pressure on them (Figs. 10 & 11). A large muscle (“#1” in Forbes 1939) has its origin on the tegumen and its insertion at the base of the socii. This muscle has been observed in all Lepidoptera studied, and acts to flex the socii and uncus (Stekolnikov 1965, Arnold & Fischer 1977).

Judging from their position, the valvae of *C. necyria* apply lateral pressure on the female terminal segments. The sacculus is elongate and fairly rigid in most Lepidoptera. Muscles originate on the sacculus and insert on the clasper of the valve. When these are flexed, the claspers squeeze the female laterally (Forbes 1939, Arnold & Fischer 1977). The valve of *C. necyria* has a membranous sacculus and lacks a clasper (Fig. 7). It may be that only the valval costa provides traction during copulation.

Eversion of the vesica is effected by the combined forces of aerostatic pressure and muscle action (Callahan 1958). In Noctuidae the cornuti appear to serve two functions (Callahan 1958, Callahan & Chapin 1960): First, while the vesica is being everted, the cornuti, which at this time point inward, help drag the formed collum of the spermatophore into the ductus bursae. Secondly, when the vesica is fully everted and the cornuti point outward, they help manipulate the spermatophore so that it properly orients in the corpus bursae. Shape and orientation of the spermatophore is extremely specific in lepidopteran species (Williams 1940, 1941, Callahan 1960). Usually its aperture is placed in close proximity to the opening of the female’s ductus seminalis. In addition, the movements of the vesica within the corpus bursae can be extremely complex. Callahan and Chapin (1960) argued that there is a “lock and key” mechanism at work during copulation that serves to inhibit mating between species. However, their research convinced them that it is not the relative shapes of the male valvae and female genitalia that is critical, as most previous authors had proposed, but is instead the configuration of the everted vesica and its ability to correctly place the spermatophore.

Unlike Noctuidae (Callahan & Chapin 1960, Takeuchi & Miyashita 1975) and Arctiidae (Stekolnikov 1965), the aedoeagus of *C. necyria* does not actually enter the female, but a small ventral tooth on the aedoeagus (Fig. 8) appears to insert into the antevaginal plate (Figs. 10 & 11). The diaphragma of *C. necyria* holds the aedoeagus tightly in place, whereas in many other Lepidoptera it is loose and allows the phallus to penetrate the female when the aedoeagus protractor muscles are activated (Forbes 1939, Stekolnikov 1965, Arnold & Fischer 1977). Opposing muscles insert on the saccus, and lack of movement of the aedoeagus in *C. necyria* may account for absence of the saccus. Judging

from the morphology of the diaphragma and aedoeagus in other diop-tids, the characteristic of having only the vesica enter the female may define a restricted group of species. In copulating *C. necyria*, cornuti of the everted vesica were in apposition with basal spines of the corpus bursae (Figs. 10 & 11). This seemed to hold male and female genitalia together even after the left valve of the male had been removed. The two sets of spines may become entangled.

During copulation, the male genitalia of *C. necyria* are withdrawn into the abdomen to a point approximately even with segment 7 (Fig. 11). This is facilitated by the long intersegmental membrane between segment 8 and the ring (Fig. 4). It would be useful to know which muscles pull the genitalia in. Their morphology may prove to be another unique feature of diop-tids and notodontids. In *C. necyria* the tergite and sternite of male segment 8 have an important holding function; when the female is pulled into the male abdomen, they appear to apply dorsoventral pressure on her seventh segment. Highly modified male eighth tergites and sternites are found in many notodontid and diop-tid species (Franclemont 1970, Holloway 1983), which suggests that a hold-ing function is typical for the group, and possibly represents a synap-omorphy for the entire lineage.

#### CONCLUSIONS

One feature of copulation seems common to all lepidopterans studied: the male uncus is inserted between the papillae anales and applies pressure on the dorsal surface of the female's postvaginal plate. Other aspects are unique to each species. The female of *Speyeria* is held at three points: the uncus secures the tergum of segment 8, valvae apply lateral pressure on the papillae anales, and the base of the valve secures sternite 7 of the female (Arnold & Fischer 1977). In *Carcharodus* the intersegmental membrane between segments 7 and 8 of the female is expanded. The uncus engages the postvaginal plate, and valvae grip the female's intersegmental membrane (De Jong 1978). There are two points of contact in *Spilosoma* and *Acrionicta*: the uncus secures the female postvaginal plate, and valvae apply lateral pressure at the base of the ductus bursae (Stekolnikov 1965). My study has shown that the female of *Cyanotricha necyria* is held in three places: the uncus engages the female postvaginal plate, valvae grasp her terminal segments laterally, and the male eighth abdominal segment applies dorsoventral pressure on female segment 7. A fourth possible point is the cornuti of the vesica, which seem to become entangled with spines located at the base of the corpus bursae, but dissection of freshly preserved material is required to confirm this.

Copulation in *C. necyria* is unique among Lepidoptera so far de-

scribed in that an exceptionally long membrane between abdominal segments 8 and 9 of the male allows the female to be pulled into the abdomen during copulation. The male eighth segment then aids in grasping the female, and may provide the majority of force for holding the pair together. This trait could prove to be another synapomorphy for the diophtid-notodontid lineage, but its distribution among species has not been adequately documented. Such information may be crucial in clarifying phylogenetic relations among these taxa.

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## A NEW SPECIES OF CATOCALA FROM THE SOUTHEAST UNITED STATES

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**ABSTRACT.** *Catocala charlottae* is described from Louisiana and Florida, the type series consisting of 100 males and 64 females. The new species is differentiated from its most similar ally, *C. alabamae* Grote, mainly by genitalic characters. Adults and genitalia of both sexes of both species are illustrated.

**Additional key words:** Noctuidae, *Catocala charlottae*, *C. alabamae*, taxonomy, underwings.

The small-bodied underwing described here, *Catocala charlottae*, closely resembles *C. alabamae* Grote both superficially and in male genitalia. *Catocala charlottae* has been taken at the type locality in Louisiana, and at several Florida localities.

Louisiana *C. alabamae* are similar to those occurring through most of its known range. A lifesize color photo of the *C. alabamae* holotype in the British Museum (Natural History) was examined and it precisely matched Louisiana *C. alabamae*.

### *Catocala charlottae* Brou, new species (Figs. 1, 2, 5, 6)

Forewing length of males averaging 19.5 mm (18.5-21.2 mm, N = 54); of females, 20.9 mm (19.7-21.8 mm, N = 32). Forewing slate gray with distinct bold black antemedial line and anal dash. Most specimens have a bold medium brown broad line paralleling basal side of antemedial line, absent above  $R_1$ . Same brown coloring evident between postmedial and subterminal line and especially noticeable as a distinct brown patch below anal dash. Brown spot at middle of costal margin above vein  $R_1$ . Reniform and subreniform present, sometimes diffuse and indistinct. Forewing underside exhibiting a pale yellow postmedial band bordered on both sides with dark brown bands. Fringe dark with darker brown bars. Basal half of forewing stronger orange-yellow than outer half with fine black line on  $Cu_2$ .

Hindwing above with black inner band and outer marginal band with connecting black-barred off-white fringe. Underside with yellow postmedial band bordered on both sides with dark brown bands. Yellow on costal half of hindwing pale, while that half along inner margin is bolder orange-yellow.

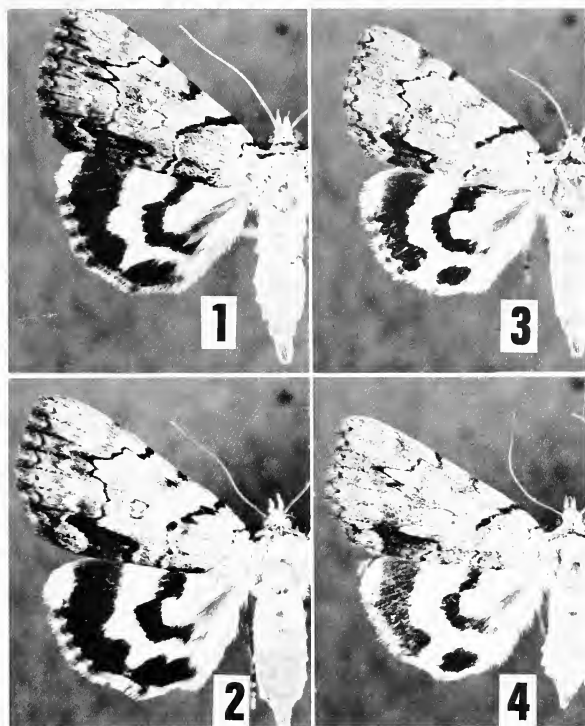
**Male genitalia** (Fig. 5) (N = 12). Cucular areas along costal margin of valva sickle shaped; mid-costal edge minimally squared, terminal edge finely serrated. Uncus semi-circular and acuminate.

**Female genitalia** (Fig. 6) (N = 10). Papillae anales elongated, strongly sclerotized. Posterior edge of lamella antevaginalis straight, abruptly angled inwardly to ostium bursae in a long narrow V-shape.

**Flight period.** At the type locality, specimens were taken at light and fermented bait from 30 April to 23 June, with peak occurrence on 22 May (N = 177). Specimens taken after the fourth week usually were worn and tattered.

**Discussion.** In Louisiana, *C. charlottae* appears on the wing about two weeks earlier than *C. alabamae*. In Louisiana, adult *C. alabamae* were taken from 13 May to 16 June (N = 38), with peak occurrence on 2 June.

Both Louisiana and Florida populations of *C. charlottae* are consistent in maculation



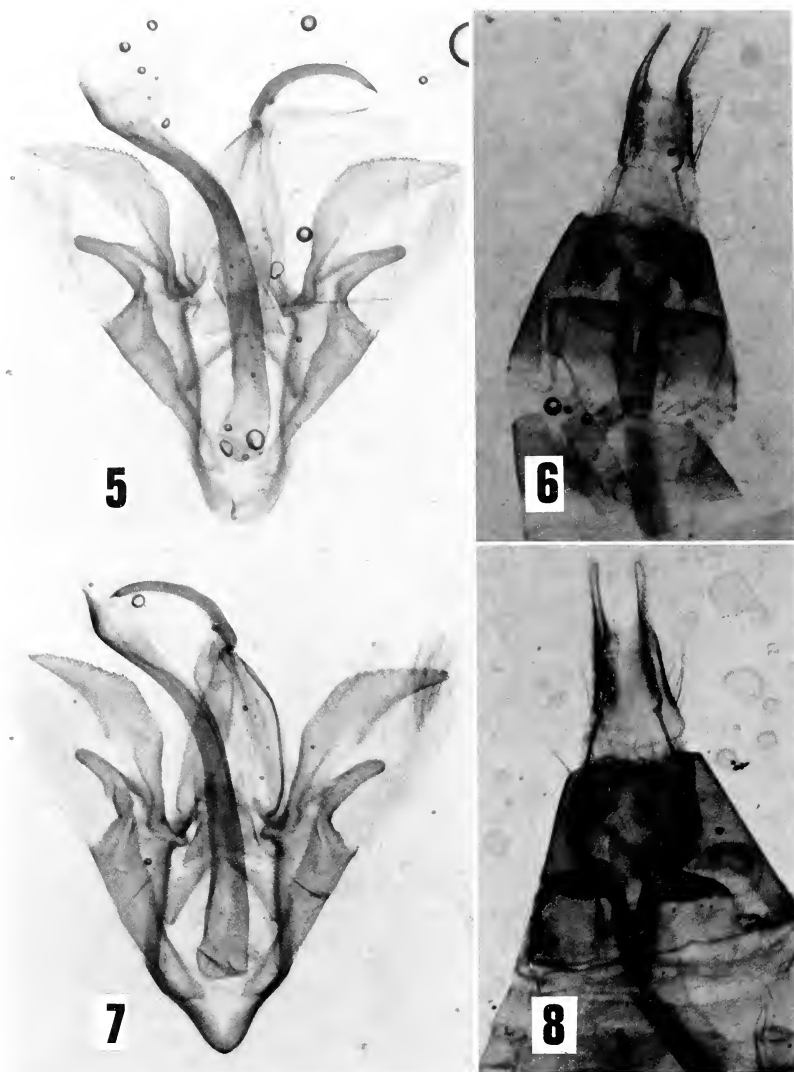
FIGS. 1-4. *Catocala* adults from the *C. charlottae* type locality. 1, *C. charlottae*, ♂ holotype; 2, *C. charlottae*, ♀ allotype; 3, *C. alabamiae*, ♂ coll. 13 May 1985; 4, *C. alabamiae*, ♀ coll. 10 June 1985.

and size; the only noticeable exterior difference is the slightly darker appearance of Florida specimens. Forewing lengths of male Louisiana *C. charlottae* (N = 108) average 7% larger than those of male Louisiana *alabamiae* which average 18.2 mm (16.6–19.5 mm, N = 20). Forewing lengths of female Louisiana *C. charlottae* (N = 32) average 9% larger than those of female Louisiana *C. alabamiae* which average 19.1 mm (17.9–20.1 mm, N = 14). The upper forewings of *C. charlottae* lack the overall blue-green suffusion present on *C. alabamiae*. Occasionally, fresh *C. charlottae* exhibit a few diffuse greenish scales around the reniform, but these are sometimes evident only with magnification.

Male genitalia of *C. charlottae* are similar to *C. alabamiae* (N = 8) except that the mid-costal margin is squared to a lesser degree in the former (Figs. 5, 7). Female genitalia of *C. charlottae* differ more noticeably from those of *C. alabamiae* (N = 6). In the latter, the posterior edge of the lamella antevaginalis is angled caudally approaching the midline and abruptly angled inwardly to ostium bursae in a wide V-shape (Fig. 8).

Since *C. charlottae* has been collected with typical *C. alabamiae* in both Louisiana and Florida localities, a distance of 660 miles (1062 km), it does not seem likely that the former is part of a phenotypic cline of the latter.

More than 30 *Catocala* species have been collected at the *C. charlottae* type locality. This habitat is a longleaf pine region, a gently rolling hilly area interspersed with flatwoods and sloughs. It is rich in diverse natural vegetation, the secondary growth being so dense that it is impenetrable except in slough areas. The *C. charlottae* larva may be a Rosaceae feeder. Four possible host species common at the type locality are *Prunus serotina* Ehrh., *Malus angustifolia* (Ait.), *Crataegus marshallii* Ellgeston, and *Aronia arbutifolia* (L.).



FIGS. 5-8. *Catocala* genitalia from the *C. charlottae* type locality. 5, *C. charlottae*, ♂ coll. 10 May 1986; 6, *C. charlottae*, ♀ coll. 15 May 1986; 7, *C. alabamiae*, ♂ coll. 2 June 1986; 8, *C. alabamiae*, ♀ coll. 3 June 1986.

*Catocala alabamiae* has the broader geographic range, occurring in Missouri, Texas, the southwestern States, the Gulf States, Tennessee, South Carolina, and Florida (Barnes & McDunnough 1918, Holland 1903:269, Sargent 1976:70, Covell 1984:315).

**Types.** Holotype ♂ (Fig. 1) 4.2 miles (6.7 km) NE Abita Springs, sec. 24, T6SR12E, St. Tammany Parish, Louisiana, 7 May 1985, V. A. Brou Jr.; allotype ♀ (Fig. 2) same data, 30 April 1985; Both in United States National Museum, Washington, D.C. Paratypes: same locality, 96 ♂, 56 ♀, 30 April to 23 June 1983-87; Jacksonville, Duval Co., Florida,

3 ♂, 5 ♀, 15 May to 7 June 1977-85; Seminole Jr. College, Seminole Co., Florida, 1 ♀, 21 May 1974; Sanford, Seminole Co., Florida, 1 ♀, 13 May 1985. Paratypes are deposited in the Florida State Collection of Arthropods, Gainesville; Louisiana State University, Baton Rouge; and the author's collection.

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BIOLOGY OF THE BLUEBERRY LEAFTIER  
*CROESIA CURVALANA* (KEARFOTT) (TORTRICIDAE):  
A FIELD AND LABORATORY STUDY

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**ABSTRACT.** Biology of *Croesia curvalana* (Kearfott) is described for the first time. Laboratory-laid eggs were white, later brown, 0.6 mm in diam., and were deposited singly under blueberry branches. Seventy-five percent hatched when given a 7-day chilling at 6°C followed by a 24-week cold treatment at 0°C. Four instars occurred during the 21-day larval development period at 21°C. Male pupal stage was 9 days, 2 days less than females. Field eggs were laid on surface litter under blueberry plants in July and August, and eggs overwintered. Flower buds were invaded by emerging larvae in the last part of April and early May, and pupation occurred during the first half of June. During four years of study, the flight season began at Blackville, New Brunswick, during the first week of July, and later at Pouch Cove, Newfoundland. Larvae from Pouch Cove were parasitized by *Chorinaeus excessorius* (Davies). In trapping experiments, virgin female *Croesia curvalana* attracted the largest proportion of males between 2200 h and 2400 h. Male *Croesia curvalana* were attracted to sex attractant lures and virgin *Choristoneura fumiferana* (Clem.) females between 2000 h and 0400 h.

**Additional key words:** Tortricidae, eggs, diel periodicity, trapping, *Vaccinium angustifolium*.

*Croesia curvalana* (Kearfott), commonly called blueberry leaftier (BBLT), are responsible for serious crop losses in Newfoundland, where lowbush blueberries, *Vaccinium angustifolium* (Ait.), are a two-million-pound export crop (Morris 1981). The insect was first recorded in Newfoundland in 1979, and subsequently reported to infest up to 30 percent of blueberry buds in 12 fields sampled in New Brunswick (G. Wood pers. comm.). Incidence of infestation is increasing due to change in blueberry cultivation practices: field burning every two years has been replaced by mowing because of rising oil prices and soil damage.

Kearfott (1907) described *Croesia curvalana*, as one of four "varieties" of *Tortrix albicomana* (Clemens) feeding on oak, rose, and huckleberry. MacKay (1962) described larval morphology based on a probable last instar. She placed it in the tribe Tortricini, genus *Argyrotoza*. Larval host plants were said to be Vacciniaceae, with distribution from Nova Scotia to British Columbia. Subsequently Powell (1964) and Hodges et al. (1983) listed the insect as *Croesia curvalana*.

In 1979 we discovered that adult male *C. curvalana* were attracted to virgin spruce budworm, *Choristoneura fumiferana* (Clemens), (SBW) adult females. Trapped moths were identified by the Forest Insect and Disease Survey (FIDS) of Environment Canada, and the Biosystematic Research Centre, Agriculture Canada. Initial trap capture of *C. curvalana* occurred in traps hung at 1.5 m above ground in balsam fir



stands. This finding suggested that some components of spruce budworm sex pheromone were also BBLT sex attractants. Sanders and Weatherston (1976) identified the primary components of SBW sex pheromone as (E) and (Z)-11-tetradecenal (96:4), and Silk et al. (1980) found traces of tetradecanal and E-11-tetradecenyl-acetate in the effluvia.

Little is known of BBLT biology. This paper describes laboratory studies from 1980 to 1983 concerning duration of egg diapause, larval, and pupal development; suitability of oviposition substrates, and fecundity. Field studies are also presented which explore the BBLT life cycle and examine diel periodicity of male attraction to calling females.

## MATERIALS AND METHODS

### Laboratory

**Egg treatment during diapause.** Eggs collected in August 1981 failed to hatch when held in the laboratory for 4 months at 21°C with temperature variations of  $\pm 2^\circ\text{C}$ . A cold treatment was therefore provided for egg collections made the next year. Sequencing of temperature and photoperiod throughout diapause in the laboratory was similar to that used for SBW (Stehr 1954). Field-collected eggs laid on dead leaves under blueberry plants were stored in Petri dishes lined with dampened filter paper, sealed with parafilm, and held at  $21 \pm 2^\circ\text{C}$  for 18 to 37 days. One batch of 1144 eggs was chilled at  $6 \pm 1^\circ\text{C}$  for 7 days in a dark refrigerator. A 2nd batch of eggs was exposed to cold treatment of  $0 \pm 1^\circ\text{C}$  in a freezer with no chilling. Samples from both batches were removed from the freezer after 18, 21 and 24 weeks. All eggs were placed in a refrigerator at  $6 \pm 1^\circ\text{C}$  for 2 days before being exposed to a constant temperature of  $21 \pm 2^\circ\text{C}$  in a 17L:7D photoperiod. Time required for eggs to hatch after removal from the freezer and percentage hatch were measured.

**Larval and pupal rearing.** After hatch, 994 larvae were transferred using a mohair brush to artificial-leaf-meal diet in plastic creamer cups (4 per cup) or to young foliage, and reared at  $21 \pm 2^\circ\text{C}$  in a 17L:7D cycle at 70% RH. Diet was that developed for SBW (McMorran 1965) as modified by Grisdale (1973), to which was added dried blueberry leaf meal (50% v/v). The meal was produced by drying and grinding previously frozen leaves from June collections. The diet was allowed to dry for a day at room temperature, which made it draw away from cup sides and provide niches for larvae. Twenty larvae were reared singly from hatch to adult emergence to determine number of larval instars and time required for maturation. Exuvial head capsules were collected and widths measured.

**Oviposition substrates.** When neonate larvae were transferred from leaves to diet, mold spores also transferred immediately contaminated the diet. Therefore, a study was undertaken to examine suitability of other oviposition substrates. In 1983, 10 newly emerged virgin females were placed with males at a ratio of 1:1.5 in each of 8 screened cages measuring 30 cm<sup>3</sup>. Moths were provided with a live blueberry branch, a 10% sucrose source, and a selection of oviposition substrates: parafilm, waxed paper, aluminum foil, filter paper strips, all 3 cm × 15 cm, and glass (2 bottles each of 21 cm surface area) which were placed on cage bottoms. In two cages, dried leaves were also offered as an oviposition substrate. Numbers and viability of eggs deposited on each substrate were determined. Cages were maintained in a 17L:7D light cycle at corresponding temperatures of 21 and 17°C with 70% RH for 3 weeks, after which eggs were counted. Eggs on the various substrates were given the cold treatment found effective in the initial diapause study, and emerging larvae counted.

**Fecundity.** Numbers of eggs produced by virgin and mated female moths under laboratory conditions were investigated. Single virgin females and male-female pairs were reared in 12-ml vials containing a 10% sucrose source. Seventy-one virgins 0 to 11 days old were dissected and their eggs counted. Females were dissected in a 5.5-cm Petri dish to expose the reproductive system. One or more drops of Shaeffer Script permanent blue-black ink diluted 50% with water was added to the preparation. Ovarioles were separated and eggs counted using a base-lit dissecting microscope at 160–400 magnification. Eggs were regarded as mature when they reached ca. 0.3 mm diam., the size at oviposition. Eggs, unfertilized and fertilized, were also counted from 31 mated 5- to 10-day-old females.

### Field

**Areas studied.** Two geographically distinct regions were selected for study. The Pouch Cove, Newfoundland, blueberry barrens, which were used in 1984 and 1985, were rocky and windswept. An area near Blackville, New Brunswick, which was used from 1980 to 1984, had less open terrain, and blueberry plants were often interspersed with ferns, small trees, and bushes.

**Life history.** In late August 1981, two weeks after the flight season, whole live blueberry plants, surrounding vegetation, and surface litter were collected at Blackville. All materials were examined in the laboratory for BBLT eggs. Samples of leaf litter were again collected from the same area in October to check for egg hatch.

Timing of insect development at Blackville was investigated in 1981. First invasion of flower buds by larvae was monitored by microscopic

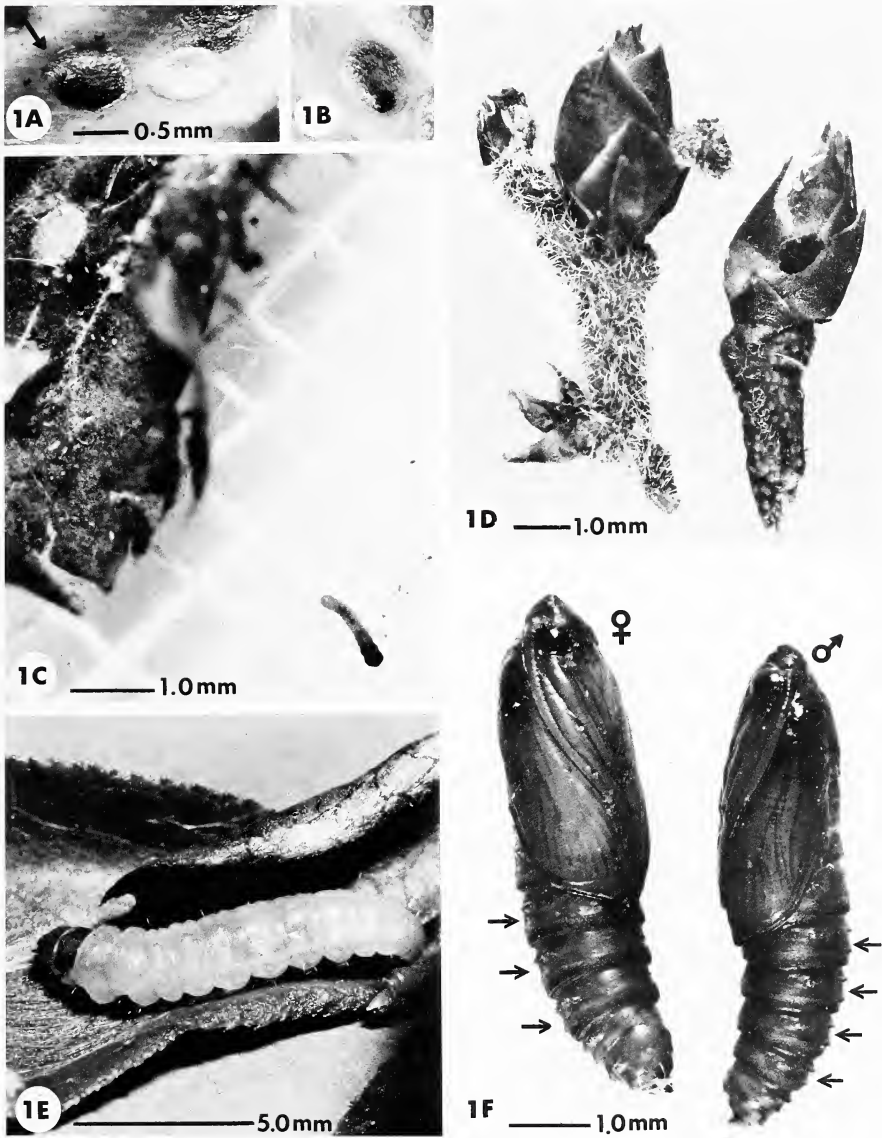


FIG. 1. *Croesia curvalana* life stages and injury to host. A, Fertile (arrow) and infertile eggs; B, Fully mature egg two days before eclosion; C, Newly emerged larva with empty egg; D, First-instar entry holes in blueberry buds; E, Fourth instar; F, Male and female pupae (arrows indicate moveable abdominal segments).

TABLE 1. Effect of chilling at  $6 \pm 1^\circ\text{C}$  and duration in freezer at  $0 \pm 1^\circ\text{C}$  on timing and success of *Croesia curvalana* egg hatch. All eggs received a post-freezer period of 2 days in refrigerator at  $6 \pm 1^\circ\text{C}$  before being incubated at  $21 \pm 2^\circ\text{C}$ .  $N = 2100$ .

No. chilling days in refrigerator	No. weeks in freezer	Percent of hatching eggs after removal from freezer				Percent hatch of eggs subjected to treatment
		5-11 days	12-18 days	19-25 days	26-32 days	
7	24	45	44	9	2	75
7	21	4	66	28	2	57
7	18	0	64	35	1	55
0	24	8	55	31	6	49
0	21	0	55	45	0	20
0	18	0	36	47	17	31

examination of blueberry plant clippings beginning in early April. Foliage was subsequently clipped for examination at two-week intervals for observations of larval and pupal development.

**Parasites.** In 1984, 528 late instars collected at Blackville and 102 from Pouch Cove were reared singly in the laboratory on foliage to determine incidence of parasitization.

**Trap height.** Height of male flight and trap height for optimal male capture were investigated at Blackville in mid-August 1980. Initial capture of male BBLT in SBW-baited traps had occurred at a height of 1.5 m. Four Pherocon® 1C sticky traps were each baited with 2 spruce budworm virgin females 0 to 24 h old in small screen cages, and 4 Pherocon® traps were left empty. Two moth-baited traps, and two empty Pherocon® 1C traps were hung 1.5 m above the blueberry canopy and 2 of each at 10 cm above the canopy. Traps were 30 m apart. Captured moths were counted each day for 10 days and the SBW virgins were replaced every 2 days.

**Flight season.** Onset and duration of the flight season was studied during four seasons in Blackville and two seasons at Pouch Cove by sweep netting and by capturing males in sticky traps. Traps were placed at canopy level in advance of the flight season and monitored every 48 h. They were baited with polyvinyl chloride (PVC) lures (Fitzgerald et al. 1973) formulated by G. Lonergan, Department of Chemistry, University of New Brunswick, to release (E) and (Z)-11-tetradecenal (95:5) with small amounts of (E)-11-tetradecanyl-acetate (0.2) at the rate of 1 SBW equivalent (Sanders 1981). These had attracted leaftier males in previous experiments (Ponder unpubl.).

**Periodicity of sexual activity.** Diel periodicity of sexual activity under field conditions was observed at Blackville between 13 and 16 July 1982 in a 96-h trapping study. Pherocon® 1C traps were each baited with one of the following: two virgin SBW females, two virgin BBLT

females, a PVC lure releasing a sex attractant at the rate of one SBW equivalent, or a blank PVC formulated without attractants. Each trap type was replicated three times within the array. Virgin SBW females were included in this experiment as lures because of their proven success in the capture of male leaftiers. Traps were separated by 30 m and their initial positions in the 12-placement array were selected by random numbers. Trapped moths were counted and traps were moved forward by 1 position every 2 h because the population was not uniformly distributed.

## RESULTS AND DISCUSSION

### Laboratory

**Egg treatment during diapause.** Three to 4 days after removal from 18 to 24 weeks in the freezer, and 2 to 3 days before hatch, a black head and larval outline could be observed inside eggs (Fig. 1B).

Significant decreases in egg mortality occurred with acclimation. Chilling eggs at 6°C in the refrigerator for one week before putting them in the freezer enhanced hatch (Table 1). The longer period of 24 weeks in the freezer resulted in significantly increased egg hatch (2-way ANOVA w/o replication,  $P < 0.05$ ). Seventy-five percent of eggs hatched if given a 24-week freezer treatment after 7 days of chilling (Table 1).

**Larval and pupal rearing.** Larvae matured through 4 instars to pupation in 21 ( $SD \pm 3$ ,  $N = 20$ ) days at  $21 \pm 2^\circ\text{C}$ . Mean head capsule widths ( $\text{mm} \pm SD$ ) progressing through instars were  $0.25 \pm 0.03$ ,  $0.35 \pm 0.04$ ,  $0.57 \pm 0.05$ , and  $1.22 \pm 0.04$ . Hatchlings were 1.2 mm long, cream colored, with a dark thoracic shield and black head (Fig. 1C). Second and third instars remained cream colored, had black heads and thoracic shields, and dark anal shields. Fourth instars (Fig. 1E) became yellow, and the head changed to cinnamon brown; the thoracic shield was cinnamon brown medially, shading to dark brown laterally. Male gonads in the fifth abdominal segment were maroon, simplifying larval sexing. Exuvial head capsules appeared slightly lighter in color than the head in the last two instars.

Mortality was high in the 994 larvae fed leaf-meal diet; only 22% survived compared with 50% on fresh foliage under the same conditions, though maturation time was approximately equal. Mortality of diet-fed larvae could be attributed in part to mold transferred with hatchlings from leaves to diet. No attempt was made to surface-sterilize eggs. Larvae did not feed on previously frozen blueberry foliage unless mixed with SBW diet. An attempt had been made in 1980 to rear 230 larvae on SBW diet without addition of blueberry meal. Three larvae survived



## Mean no. mature eggs per female

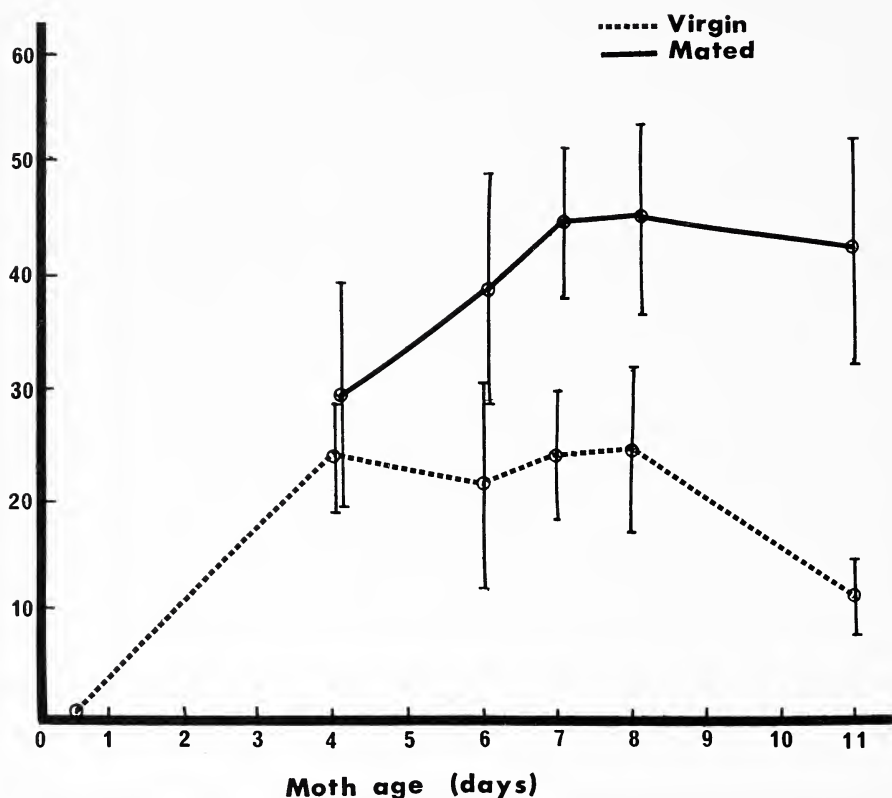


FIG. 2. Numbers of mature eggs in mated ( $N = 31$ ) and virgin ( $N = 71$ ) female *Croesia curvalana* in relation to age. Vertical bars indicate SD.

to pupation, and larval development time was 75 to 80 days. Newly hatched larvae seldom burrowed into flower buds (Fig. 1D) on diet, but rather spun nests between the diet and creamer cup wall.

Pupation occurred either in spun nests between diet and creamer cup wall, or under the lid. Males pupated before females, and mean male pupal duration was  $9.2$  ( $SD \pm 0.8$ ,  $N = 20$ ) days which was shorter by 2 days than mean female pupal duration of  $11.5$  ( $SD \pm 1.3$ ,  $N = 20$ ) days. Male pupae could be distinguished by presence of a fourth moveable abdominal segment (Fig. 1F), females having only three moveable segments.

**Oviposition substrates.** Few eggs were deposited by BBLT females in the laboratory. Such eggs were scattered singly on materials placed in cage bottoms. Eggs were white, flattened, convex, 0.6 mm in diam.,

and had a clear pebbled surface. Within a week they changed to reddish brown as the enclosed embryo matured (Fig. 1A). In total, 1061 eggs were collected in 1983 on synthetic substrates, 44% on waxed paper, 37% on parafilm, 8% on aluminum foil, 7% on filter paper, and 4% on glass. No preference was shown for dried leaves as an oviposition substrate. Egg maturation and hatch after diapause was 66% on waxed paper, and 64% on filter paper, but only 32% on parafilm. Other substrates resulted in less hatch.

**Fecundity.** No mature eggs were found when 5 newly emerged virgins were dissected; however, a mean of 90.8 (SD  $\pm$  11.4) immature eggs were counted. In mated females, ca.  $\frac{1}{3}$  of eggs matured by the 4th day (Fig. 2), and up to 50% matured by the 7th day after emergence. Twenty-six percent matured by the 7th day in virgins. Both mated and virgin females laid few eggs in vials. A total of 4 unfertilized eggs laid by the 71 virgins remained white. Fifty-five fertile eggs which changed from white to brown were laid by the 31 mated females.

Decrease in numbers of eggs in virgin females between days 8 and 11 (Fig. 2) suggested that their eggs were resorbed. Most moths (79%) died between 11 and 12 days after emergence; however, some lived 15 days.

Many factors contributed to the difficulty of rearing this insect on artificial-meal diet. Fecundity was low. The preferred oviposition substrate was ill-defined, and many substrates proved unsuitable for complete egg maturation. Hatchlings were small, delicate, and difficult to locate even with a microscope. Year-round rearing of BBLT using fresh vegetation would be impractical without light- and temperature-controlled greenhouse and refrigeration for continuous propagation of blueberry plants.

### Field

**Life history.** Eggs were laid singly on dried leaf litter under blueberry plants, and were difficult to locate even with a microscope. No eggs were located on living plant leaves, stems, or branches. October collections of eggs indicated that hatch had not yet occurred. Seventy-five percent of field-collected eggs hatched successfully in the laboratory when given a treatment of 1 week at 6°C and 24 weeks at 0°C. These findings indicate that eggs overwinter. Blueberry cultivation practices that incorporate field mowing rather than burning may therefore result in increased leaf-tier populations.

Foliage clipped weekly from April to mid-June at Blackville indicated that infestation of flower buds by first-instars occurred during the last two weeks of April (Table 2). Larvae burrowed into closed flower buds leaving a round hole marked by an accumulation of yellow frass. Fre-

TABLE 2. Development of *Croesia curvalana* larvae, Blackville, N.B., 1981.

Date	Stage of blueberry foliage	No. larvae collected	Instar no. or stage
18 April	Closed buds	0	
24 April	Closed buds	6	1
6 May	Expanded flower buds	327	1
12 May	Expanded leaf buds	121	1
		129	2
22 May	Young leaves	62	2
		102	3
2 June	Expanded leaves and flowers	247	3
		153	4
12 July	Flowers and immature fruit	2	4
		187	pupae
		15	pupal cases

quently, two larvae were found feeding in the same bud. Larvae subsequently fed on swelling leaf buds. Numbers of buds infested with larvae increased to mid-May, indicating a three-week period of egg hatch. Visible plant damage peaked just before larvae pupated. At this time, terminal leaf growth was webbed and eaten, and larger leaves were folded or webbed together to form shelters. Increased numbers of abandoned shelters during late-instar development suggested that larvae moved frequently.

First appearance of pupae in the field at Blackville ranged from the first to third weeks in June. Males pupated before females. The dark brown pupae could be found sandwiched in shelters or occasionally hanging freely by the cremaster from blueberry twigs.

The moths were 5 to 7 mm long, and were of a yellowish hue with forewing markings of rust and yellow. Toward the end of the flight season, spent moths lost many wing scales, which made them appear cream colored. First male moth emergence at Blackville, as established by trap capture, occurred during the first week of July in all four years of study. It occurred thus regardless of differences in weather during the larval and pupal stages. Sweep-net collections indicated that, as in the laboratory, males emerged before females. Sweep-net collections were achieved two to three days after first male trap capture. First sweep-net collections had a male:female ratio per sweep of 0.116:0.044, which changed to 0.009:0.008 by the end of the flight season. At Pouch Cove where the population was higher, the ratio changed from 0.23:0.02 to 0.22:0.16 by the end of the flight season. Moth location may have had a bearing on results. At Blackville where mean day time temperatures were 5°C higher than Pouch Cove, moths preferred shad-

TABLE 3. Trap capture of male *Croesia curvalana* in Pherocon® 1C traps hung at different heights in 10 days, Blackville, N.B., 1980. Number of traps = 8.

Trap height above blueberry canopy	Mean 24-h catch per trap by virgin spruce budworm	Mean 24-h catch per unbaited trap
1.5 m	6.0	0.1
10 cm	17.6	0.7

ed areas, while at Pouch Cove where the barrens had mean wind velocities of 21.6 km/h and mean RH of 82%, moths were located in sheltered areas of deep vegetation. Female moths may have been at a lower stratum or beneath vegetation during oviposition, making sampling for females by sweep-net unreliable.

Length of flight season in the 4 years of study at Blackville ranged from 30 to 47 days; at Pouch Cove, it began in 1984 on 12 July and lasted 35 days in 1984, and in 1985 on 19 July and lasted 28 days.

**Parasites.** Larvae collected at Blackville were parasitized 10% by tachinid flies which emerged as larvae from their hosts. Tachinid puparia were held in the laboratory for eight months without a cold period. One fly emerged in too poor condition to identify. No tachinids were found in larvae from Pouch Cove. Two ichneumonids emerged as adults from pupae collected as larvae at Pouch Cove. These were identified by the Biosystematic Research Centre, Agriculture Canada, as *Chorinaeus excessorius* Davies. This parasite has not been reported previously from BBLT.

**Trap height.** Significantly more male BBLT were captured in traps hung at 10 cm than at 1.5 m above the foliage in both unbaited and virgin SBW baited traps  $\chi^2_c = 109.3$ ,  $P \ll 0.001$ ,  $df = 1$ ) (Table 3) which confirmed visual observations that moths flew immediately above the foliage.

*Croesia semipurpurana* (Kft.), a species morphologically similar to *C. curvalana*, is attracted to traps hung at 1.5 m baited with components (Grant et al. 1981) which are also part of the spruce budworm sex pheromone bouquet.

**Periodicity of sexual activity.** The largest proportion of BBLT males trapped by all bait types was between 2200 and 0200 h (Table 4). Virgin BBLT females captured the largest proportion of BBLT males from 2200 to 2400 h ( $P = 0.05$ , Chi square for multiple proportion, Zar 1984) indicating that female sex pheromone release (calling) took place during these hours. PVCs which released attractant continuously over a 24-h period attracted BBLT males consistently between 2000 and 0400 h, suggesting that male flight period and attraction to lures may extend

TABLE 4. Proportion of 96-h trap capture of male *Croesia curvalana* by 2-h intervals at Blackville, N.B., 1982. Baits in Pherocon® 1C traps were replicated 3 times (N = 1513). No moths were captured between 1000 and 1400 h.

Bait	Trapping interval (h) (AST)									
	1400- 1600	1600- 1800	1800- 2000	2000- 2200	2200- 2400	2400- 0200	0200- 0400	0400- 0600	0600- 0800	0800- 1000
Two virgin BBLT	0.00	0.00	0.00	0.08	0.55	0.27	0.02	0.02	0.02	0.05
Blank PVC	0.11	0.00	0.00	0.04	0.44	0.33	0.04	0.00	0.04	0.00
PVC sex	0.01	0.01	0.01	0.26	0.30	0.30	0.11	0.01	0.01	0.00
Two virgin SBW	0.00	0.00	0.00	0.23	0.57	0.16	0.03	0.00	0.00	0.01

on either side of the virgin female BBLT calling period. This was confirmed by the finding that virgin female SBW, which would have been calling from 2000 h to 2400 h (Palaniswamy & Seabrook 1985), also attracted BBLT males before the BBLT female calling period.

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## HYLESIA ACUTA (SATURNIIDAE) AND ITS AGGREGATE LARVAL AND PUPAL POUCH

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**ABSTRACT.** Developmental stages of *Hylesia acuta* are described and illustrated, and two examples of aggregate larval and pupal pouches are reported. Larval development from eggs gathered in Chiapas, Mexico, required ca. 80 days at 25-32°C. Late instars constructed a tough, silk pouch where they remained by day, emerging to feed at night. The first instar is pale yellowish tan with a black head; the mature larva is dark saffron mottled with green. All instars possess urticating spines, but not adults. Larvae constructed individual cocoons before pupating together in the pouch, in which they remained for eight months before emergence. A wild pupal pouch found in Veracruz, Mexico, contained 46 pupae from which 42 adults emerged. A dissected female yielded 374 ova. The species appears to be univoltine, adults emerging during the tropical wet season.

**Additional key words:** Mexico, silkmoths, immature stages.

The American genus *Hylesia* contains about 100 species of small silkmoths (C. Lemaire pers. comm.), the biology of most unknown. The genus has achieved notoriety in parts of South America because of urticating abdominal hairs of some females (Lamy & Lemaire 1983) used to cover egg masses (Gardner 1982). Hairs in some species cause severe dermatitis in man (Pesce & Delgado 1971, and others).

In the Central American *Hylesia lineata* Druce, ova pass the dry season in a felt nest (Janzen 1984). Though *H. nigricans* Berg, whose immature stages and behavior were illustrated by Lampe (1986), also has overwintering eggs, at least several other species do not (Gardner 1982). Pupation is solitary in most known species.

Aggregate pupation above ground in a silk pouch is unusual among Saturniidae. A "communal cocoon" of an unidentified species of *Neodiphthera* (Saturniinae) from New Guinea contains about a dozen cocoons (R. S. Peigler pers. comm.). Stoll (1791) illustrated a "gregarious cocoon" ascribed to *Phalaena Bombyx bibiana*, which Bouvier (1925) believed was a *Hylesia* (Hemileucinae) species. Beutelspacher (1985) found *Hylesia frigida* Schaus gregarious larvae and pupae in loose silk pouches in Mexico. Cockerell, in Packard (1914), quoted Dyar as having a specimen of *Hylesia tapabex* Dyar "bred from a 'gregarious podlike cocoon.'" Bouvier (1924a, 1924b, 1925) described two aggregate pupal pouches of this species from Venezuela. A nest of *H. tapabex* is preserved in the Muséum national d'Histoire naturelle, Paris (C. Lemaire pers. comm.). The present study establishes that *Hylesia acuta* Druce, closely related to *H. tapabex*, also pupates in a shared pouch.

*Hylesia acuta* is a small moth (forewing length 2.5-3.1 cm) with marked sexual dimorphism, the female resembling many *Hylesia* species,

while the male is distinctive (Fig. 3). Described by Druce (1886) from "North Mexico," its known range extends along the eastern and western lowlands of central Mexico S into Guatemala and E into Yucatan and British Honduras (Schüssler 1934, Hoffmann 1942, C. Lemaire pers. comm.). Its biology and aggregate pupation behavior have not been previously reported.

#### REARED MATERIAL

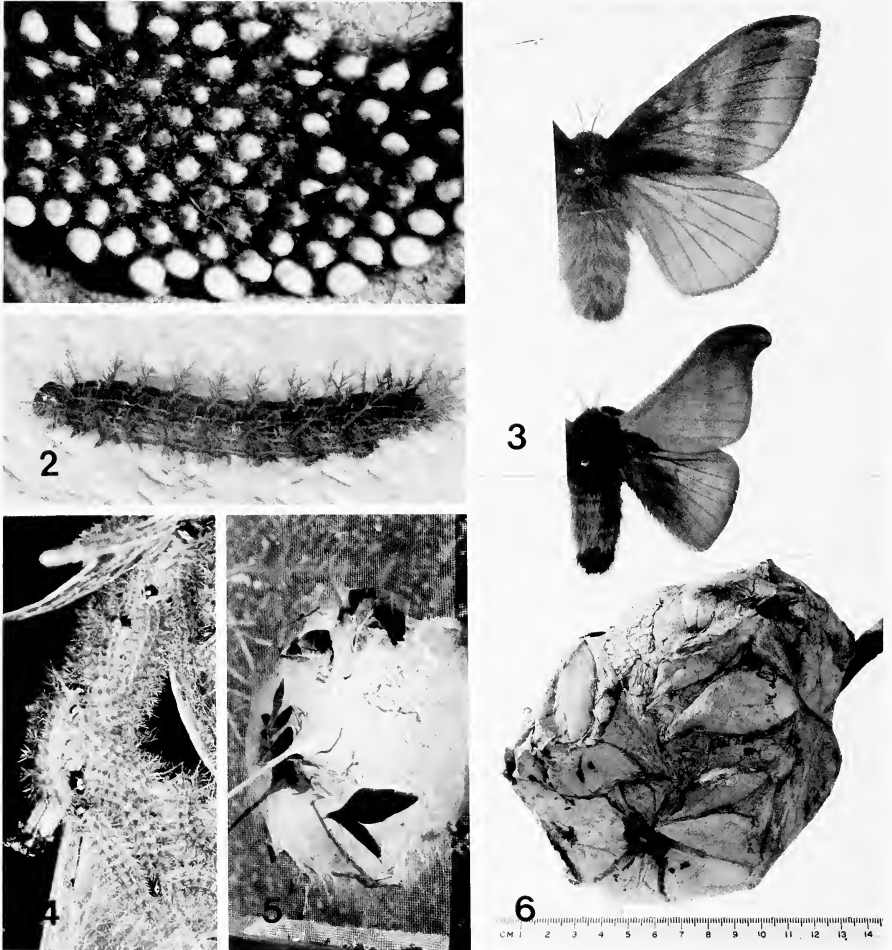
A wild female captured near Huixtla, Chiapas, Mexico, oviposited in a paper bag on 10 July 1983. The eggs were white, upright ovals placed in a single-layered dense cluster, partially hidden with brown abdominal hairs (Fig. 1). They numbered ca. 100. Refrigerated at ca. 50°C for 8 days to delay hatching, the eggs were then kept in a covered plastic petri dish under natural daylight at temperatures varying between 25 and 32°C. They hatched in 25 days, and were transferred to a tight styrene box 11 × 11 × 4 cm. During the first week they refused to feed on any plants offered, instead eating eggshells. Occasionally they wandered in single file, returning to the nest without feeding. Eventually most did accept Brazilian pepper tree, *Schinus terebinthifolius* Raddi (Anacardiaceae). Plants refused included plum, *Robinia pseudoacacia* L., *Rhus laurina* Nutt., *Quercus agrifolia* Née, and others. Larvae were then placed on small pepper tree branches in a container of water in a screened cage in a humid greenhouse at 25–32°C, with foliage replaced daily. From the earliest stages they spun a loose silken platform to which they returned after group wanderings or feeding.

Six weeks after hatching, the half-grown larvae spun a silk tent at the end of a branch. It appeared as a small, broad cone (ca. 7 cm diam.), of dense silk tipped on its side. A hole near the vertex allowed larval access; frass fell through a slit at the bottom.

When the tent was completed, the larvae became nocturnal, not appearing until at least 1 h after dark when they emerged and traveled in single file, stopping to feed in densely packed rows on mature (darker) leaves. Such tandem movement in early instars is typical among hemileucines as noted in *Hemileuca oliviae* Cockerell (Capinera 1980), *Hylesia lineata* (Janzen 1984), and other species (Lemaire 1971).

The earliest instars were pale yellowish tan, with typical hemileucine spination retained by all subsequent instars (Figs. 2, 4). This color deepened, and after the fourth instar was dark saffron indistinctly mottled with green. One dorsal and two subdorsal longitudinal stripes were straw colored. Mature larvae were plump (Fig. 2). Instar duration and number were not determined.

Half-grown larvae became diurnally active during two days as they spun a larger tent (ca. 15 cm diam.). Incorporating material from the



FIGS. 1-6. *Hylesia acuta*. 1, Eggs partially hidden by female abdominal hairs; 2, Mature larva; 3, Adult female (upper) and male (lower); 4, Early instars feeding on *Schinus terebinthifolius*; 5, Aggregate larval and pupal "nest" pouch of captive reared larvae; 6, Pouch containing wild pupae.

first tent, its walls resembled thin leather, shiny on the inside, and white on the outside (Fig. 5).

Larvae molted within the tent, and the cast-off skins fell through the bottom slit. Shortly before pupation larval mortality increased. Five survivors ceased feeding at 10 weeks, reaching a length of ca. 50 mm. A flashlight beamed through the tent at night revealed their silhouettes, which became progressively less visible as they worked during three weeks to fill it with firm, woolly white silk. Four small holes or "escape"

tunnels to the outside were made, two by larvae chewing through the cage's fiber glass screen where it adhered to the pouch.

By 1 December noticeable larval activity had ceased. Several weeks later, the pouch was opened, revealing a small mass of cocoons imbedded in silk. From hatching to pupation was ca. 80 days. The next year in the first week of August, five imagines emerged.

#### WILD MATERIAL

A cordiform pupal pouch of *H. acuta* with viable pupae was found near Papantla, Veracruz, Mexico, in a small, dead tree ca. 4 m above ground on 27 July 1986. Surrounded by a fresh growth of tall grasses, the tree appeared to have been *Bursera simaruba* (L.) Sarg. (Burseraceae). Imprints of fresh leaves were imbedded on the surface of the pouch. The pouch measured  $13.0 \times 9.5 \times 5.0$  cm, and contained 46 pupae. It had been constructed during the previous wet season, since a new wet season was just beginning.

This pouch was angular (Fig. 6), and possessed three widely spaced holes on its upper surface, providing access for feeding larvae and exits for emerging imagines.

Inside, pupae were arranged in double-walled, fusiform cocoons, tightly fit and adhering to one another. Cocoons were parallel in a band three layers thick which wrapped around the supporting branch within the pouch. Exit vents were oriented upward, and opened on several smooth-lined corridors through the dense silk wool to the outside openings of the pouch.

The pupae conform to Bouvier's (1924a, 1924b, 1925) description of *Hylesia tapabex*. He pointed out that while *H. tapabex*, known to pupate aggregately, does not possess a cremaster, solitary pupating *Hylesia* species do possess one. This is further evidenced in the solitary pupae of *H. nigricans* (Lampe 1986) and *H. lineata* (pers. obs.) which possess cremasters.

Emergence of imagines began in September. From 46 pupae, 19 males and 23 females emerged during three weeks. Average emergence was at 1715 h PDT (SD = 1554–1836 h PDT,  $n = 9$ ). Notably, no parasitism was found. Numerous attempts were made to achieve matings between emerged siblings without success.

Observations of captive females suggest that *H. acuta* oviposits three or more clusters. Dissection of a newly emerged female yielded 374 ova. Females produced no stinging when their abdomens were rubbed on the author's skin.

Voucher imagines are in the San Diego Museum of Natural History, and collections of C. Lemaire, S. Stone, M. Smith, D. Herbin, and the author.



## DISCUSSION

*Hylesia* are among the smallest American saturniids. Those that live under extreme seasonal conditions have evolved strategies to survive the harsh conditions of a dry season (Janzen 1984). In *H. acuta*, a protective nest has evolved in which pupae survive the dry season. The tough, leathery pouch filled with silk wool protects them against adverse weather and perhaps parasites. Its light silvery gray color reflects heat, and its resemblance to a wasp nest may discourage avian predation.

Published records (Beutelspacher 1978), correspondence (C. Lemaire pers. comm.), and labels of wild collected specimens indicate dates of capture predominately from June through August, with records as late as September, during the season of heaviest rains.

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## EUROPEAN CORN BORER REPRODUCTION: EFFECTS OF HONEY IN IMBIBED WATER

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**ABSTRACT.** European corn borer adults are well known to imbibe water, without which their reproduction is greatly decreased. Whether their reproduction is enhanced by sugars in imbibed water has long been unresolved. Two groups totalling more than 50 captive fertile pairs, one group receiving 15% honey-water to imbibe, the other plain water, were compared with respect to 10 reproductive attributes. Honey in imbibed water significantly improved performance in four attributes, resulting in heavier eggs, more females maintaining or increasing egg weight during the oviposition period, fewer females with immature oocytes at death, and more unlaidd eggs that were mature. Adult nutritional ecology seems a potential factor in the dynamics of populations.

**Additional key words:** *Ostrinia nubilalis*, Pyralidae, Pyraustinae, fecundity, egg weight.

Imbibing of water by adults of the European corn borer, *Ostrinia nubilalis* (Hübner), is well documented (Vance 1949). Imbibed water greatly increases adult lifespan and fecundity; without it, reproduction is severely depressed (Barlow & Mutchmor 1963, Kira et al. 1969). Concerning sugars in imbibed water, reported effects are contradictory, one paper claiming no further improvement in reproduction (Caffrey & Worthley 1927), and another claiming the opposite (Kozhantshikov 1938). Unfortunately, the first paper offers no supporting data, and the second enumerates data insufficiently for independent assessment. Although this contradiction has never been addressed, the prevailing view, as reflected in mass rearing practice (Reed et al. 1972), is that sugars in imbibed water do not enhance reproduction. Clarification seems desirable for at least two reasons. First, European corn borer adults aggregate in grass and weedy vegetation bordering host fields (Showers et al. 1976), where potential adult food sources such as nectaries and honeydew-producing insects may occur. Second, if sugars do enhance reproduction, mass rearing programs might thereby increase production with little extra effort.

Here I report how European corn borer adults receiving honey-water and plain water performed in the 10 reproductive attributes listed in Table 1.

### MATERIALS AND METHODS

One experiment was done. In it, 78 single female-male pairs of pupae were numbered, and the 39 even-numbered ones assigned to the treatment group, and the 39 odd-numbered ones to the control group. After adults eclosed, treatment pairs received honey-water to imbibe, control

pairs plain water. After all moths had expired, reproduction data gathered from both groups were compared.

Pupae were obtained from a culture at the University of Minnesota originating in Iowa and maintained according to standard European corn borer production methods (Reed et al. 1972). The pupae were sexed, and pairs placed in 1-pint (0.47 liter) cardboard ice cream containers capped with Petri dish lids. Lids were lined with waxed paper to ensure a surface suitable for oviposition. Containers were kept in a walk-in environmental chamber programmed for 16 h light at 27°C and 8 h dark at 17°C, both at 60% RH.

Each container had a 35 cm<sup>3</sup> foam-latex sponge that dispensed distilled water in the control group and 15% (by volume) honey-water in the treatment group. Sponges and liquids were renewed every second day. Honey was used as the sugar source because in composition (White 1975) it conveniently simulates hexose-rich shallow-flower nectar (Baker & Baker 1983) and insect honeydew (Auclair 1963).

Reproduction data were gathered once daily near mid-day. Mating and fertilization success was ascertained by holding one or several early egg masses for a week or until the dark larval heads showed through chorions. Preoviposition period was measured from female eclosion to first oviposition; such data were used only when the male of the pair eclosed no later than one day after the female because late male eclosion prolonged the period.

"Early eggs" refers to eggs laid on the first or second day of oviposition, "late eggs" to eggs laid on the fourth to eighth day of oviposition. Mean egg weight was determined from one or more masses totalling 17 to 184 eggs removed intact from the waxed paper and weighed to the nearest 0.5 mg. Mature unlaid eggs were counted in excised ovaries at stereomicroscope magnifications up to 65 $\times$ . Maturity of unlaid eggs was judged by size and chorionation. Eggs were deemed chorionated if they did not readily absorb 0.3% aqueous methylene blue after 3 min exposure (Jennings 1974). Immature oocytes in expired females could not be counted accurately, so only their presence or absence was recorded. Only data from fertile pairs were analyzed because some reproductive attributes are atypical in the absence of insemination.

Referral of species mentioned in this paper to Pyraustinae is based on the classification of Fletcher and Nye (1984).

## RESULTS AND DISCUSSION

Of the 78 pupal pairings, 79% resulted in fertile eggs, a level believed high enough to provide representative adult performance. Data were analyzed from fertile pairs numbering 25 and 27 in the plain-water and honey-water groups, respectively, these numbers also reflecting

losses from mishaps like moth escapes. The fewest number of observations on any attribute in either group was 19 for preoviposition period in the water-imbibing control, reflecting a further loss of data on this attribute resulting from late male eclosions.

Four differences between the two imbibing groups were significant (Table 1). Thus, in the honey-water group, a greater proportion of unlaidd eggs was mature, fewer expired females contained immature oocytes, late eggs were heavier, and more females maintained or increased egg weight during the oviposition period. The first and second differences suggest that honey-water imbibers approached full reproductive potential more closely than plain-water imbibers. The third and fourth differences presumably reflect conversion of glucose and fructose in honey to lipid that became incorporated into oocytes during egg maturation (Kozhantshikov 1938, Downer & Matthews 1976). Consequences of differing egg weights have not been investigated in the European corn borer, but in other moth species, heavier eggs produce larvae more likely to survive (Barbosa & Capinera 1978, Harvey 1985). Hence, sugars in imbibed water might enhance European corn borer fitness if females live long enough to lay the heavier eggs. Some do live long enough (Elliott et al. 1982): in 9 of 14 samples taken from June to September,  $\frac{1}{6}$  of wild mated females were 4 or more days old, the onset age for heavier eggs in the present study.

Although 6 of the 10 reproductive attributes did not differ significantly between imbibing groups ( $P \geq 0.06$ , one-tailed Student *t*-tests), all attributes except female lifespan show differences of 1 to 150% in favor of the honey-water group (Table 1). Shorter female lifespan in the honey-water group seems anomalous, but no cause was evident. Despite this attribute, the honey-water group outperformed the plain-water group in an overall comparison of reproduction as follows. Of eight independent attributes (omitting number of unlaidd mature eggs and percentage females maintaining or increasing egg weight, which are facets of other attributes), seven show gains resulting from honey imbibing whether individually significant or not, and such an outcome is not likely due to chance ( $P < 0.05$ , one-tailed sign test).

Because European corn borer fecundity varies directly with body size (Vance 1949), the possibility that body-size differences between imbibing groups caused attribute differences was examined. Vance (1949) did not express the relation mathematically; he tabulated six class means for number of eggs laid (*y*) and corresponding initial adult female weight (mg) (*x*). Based on retrospective frequency-weighted analysis of class means, the relation can be quantified as  $y = 8.5x + 153$  (66n,  $r^2 = 0.88$ ,  $P < 0.001$ ). The correlation coefficient is overestimated because it is derived from means rather than individual values,



TABLE 1. Reproductive performance of European corn borer adults receiving plain water and 15% honey-water. Means and percentages are based on 19 to 27 observations per treatment group.

Attribute	Mean ( $\pm$ SD) or percentage		% change due to honey
	Plain water	Honey-water	
Lifespan, days			
Female	17.5 $\pm$ 5.4	16.5 $\pm$ 5.4	-6
Male	16.8 $\pm$ 4.0	18.2 $\pm$ 4.5	8
Preoviposition period, days	2.8 $\pm$ 1.3	2.3 $\pm$ 1.2	-18
No. mature oocytes			
Laid	601 $\pm$ 191	623 $\pm$ 237	4
Unlaid	28 $\pm$ 38	50 $\pm$ 53*	78
Total	630 $\pm$ 170	673 $\pm$ 209	7
% females containing immature oocytes at death	86	53*	-38
Egg weight, mg			
Early eggs	0.0638 $\pm$ 0.0048	0.0643 $\pm$ 0.0060	1
Late eggs	0.0618 $\pm$ 0.0066	0.0652 $\pm$ 0.0070*	6
% females maintaining or increasing egg weight	24	60*	150

\* Significantly different ( $P < 0.05$ , based on one-tailed Student *t*-tests for means;  $2 \times 2$  contingency tables and adjusted-G tests for numbers underlying percentages).

but the relation is nevertheless striking. Such a relation could not have affected attribute differences in the present study for two reasons. First, length of one forewing, a surrogate for body weight (Miller 1977), averaged 13.5 (SD  $\pm$  0.6) mm and 13.4 (SD  $\pm$  0.8) mm in females of the plain-water and honey-water groups, respectively. These means are identical statistically, the difference, 0.1 mm, being less than 1% of either. Second, in neither imbibing group did any egg attribute correlate significantly with female forewing length ( $r^2 < 0.08$ ,  $P > 0.20$ ).

In virgin European corn borer females, 80 egg follicles have been seen in one ovariole (Drecktrah & Brindley 1967). This number translates to 640 per female, near the average total number of mature eggs per female in the present study (Table 1). Number of oocytes already mature at female eclosion averaged 92 (SD  $\pm$  16, 4n) in the present study, as determined for females 0-4 h old averaging 14.0 mm in forewing length. Subtracting 92 from total mature eggs in the plain-water and honey-water groups leaves 538 and 581 eggs, respectively. The latter numbers suggest that more than 80% of oocytes mature after females eclose (538/630 = 0.85; 581/673 = 0.86), and that ample opportunity exists for adult nutrition to enhance oogenesis.

Although European corn borer adults have not been reported to

imbibe sugary liquids in the wild, it is possible they do so opportunistically because adults of other Pyraustinae use such liquids. Both sexes of *Pyrausta orphisalis* Walker have been seen taking nectar from flowers (Campbell & Pike 1985). In *Cnaphalocrocis medinalis* (Guenée), imbibed sugars and planthopper honeydew greatly increased adult lifespan and fecundity (Waldbauer et al. 1980). Moreover, both sexes of European corn borer have well developed proboscides: females with forewing length (w) averaging 14.0 mm had proboscides with uncoiled length (p) averaging 7.3 mm (4n), forming a p/w ratio of 0.52. This length of proboscis could provide access to floral nectar of many kinds of plants, and the ratio is well within the range signifying flower visitation in other lepidopterans (Opler & Krizek 1984:31).

In conclusion, some differences in reproductive attributes between treatment groups are subtle. They nevertheless bring one step nearer resolution the old uncertainty whether sugars in imbibed water affect European corn borer reproduction. The adult's use of sugary liquids in nature remains to be shown. If it is shown, adult nutritional ecology could be a factor in the dynamics of populations, with sugar consumption perhaps elevating population quality and crop damage. Such an outcome could lead to removal of natural sources of sugar as a supplemental management technique for the insect.

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## GENERAL NOTE

### PARASITOID AND HOSTPLANT RECORDS FOR GENUS *SCHINIA* (NOCTUIDAE) IN TEXAS

**Additional key words:** *Schinia bina*, *S. arcigera*, *S. chrysella*, Tachinidae, Hymenoptera.

In an earlier report, R. S. Peigler and S. B. Vinson (1984, Southw. Entomol. 9:48-51) listed 24 species of *Schinia* Hübner collected in Brazos Co., Texas, and commented on abundance of the adults. The present paper deals with some observations on the immature stages. The life-cycle for most species is as follows: eggs are deposited in autumn into flowers of composites (Asteraceae), most species specializing on one or a few host genera. Larvae mature in less than one month, pupation is below ground, and adults emerge the following autumn. Peak abundance of larvae as well as adults is in fall.

We experienced difficulty in associating field-collected larvae with adults because diapause was not terminated by various treatments, and pupae often died before adults emerged. Reared material emerged at the next normal flight time for some species, but this was the exception. A few pupae produced adults only after being held for two or more years. Some parasitoids were equally delayed in emerging as adults. Consequently, some records below are cited as "*Schinia* sp." where we were unable to associate larvae with adults. Interspecifically, *Schinia* larvae are as variable as adults in color and pattern (Covell, C. V. 1984, A field guide to the moths of eastern North America, Houghton Mifflin, Boston, Pl. 29), but larvae can confidently be assigned to this genus based on general appearance.

Previously published records of parasitism in *Schinia* are few. P. H. Arnaud (1978, A host-parasite catalog of North American Tachinidae (Diptera), U.S. Dept. Agr. Misc. Publ. 1319, 860 pp.) listed only one record for a tachinid attacking *Schinia*: *Winthemia quadripustulata* (Fabricius) parasitizing *Schinia septentrionalis* Walker (= *S. brevis* Grote). Only one record for a hymenopterous parasitoid attacking *Schinia* was cited by P. M. Marsh (in Krombein, K. V., P. D. Hurd, D. R. Smith, B. D. Burks (eds.), 1979, Catalog of Hymenoptera in America north of Mexico, vol. 1:263, Smithsonian Press, Washington, D.C.): the braconid *Cardiochiles magnus* Mao in *Schinia* sp. Another braconid, *Microplitis croceipes* (Cresson) (det. by P. M. Marsh) was reared from *Schinia olivacea* J. B. Smith collected in Live Oak Co., Texas, and another tachinid, *Gymnoclytia unicolor* Brooks (det. C. W. Sabrosky) from *Schinia olivacea* in Bexar Co., Texas (R. O. Kendall pers. comm.).

Our larvae were collected in or on composite inflorescences. They were kept individually in the laboratory on artificial diet (Vanderzant, E. S., C. D. Richardson & S. W. Fort 1962, J. Econ. Entomol. 55:140) in plastic shell vials plugged with cotton. It was necessary to isolate larvae to prevent cannibalism, a problem also noted by D. F. Hardwick (1958, Can. Entomol. Suppl. 6:1-116). For hostplants, we follow nomenclature of D. S. Correll and M. C. Johnston (1970, Manual of the vascular plants of Texas, Texas Research Foundation, Renner, Texas, 1881 pp.). All records below are from Brazos Co., in E-central Texas. Species of *Schinia* most commonly collected by us in the larval stage were *S. bina* (Guenée), *S. arcigera* (Guenée), *S. chrysella* Grote, and *S. bifascia* Hübner. Also, many larvae of *S. nundina* (Drury) were collected from flowers of goldenrod (*Solidago* spp.) in October, but few adults were because they are rarely phototactic.

The following parasitoids were reared:

#### Diptera

##### Tachinidae

*Plagiomima similis* (Townsend). One specimen reared from larva of *Schinia bina* collected in fall. Puparium formed outside host and overwintered before emerging.

*Eucelatoria* sp. (*armigera* Coquillett of authors). One specimen reared from *Schinia* sp. Puparium formed outside host, adult emerged in fall without diapausing.

*Winthemia rufopicta* (Bigot). One specimen reared from *Schinia* sp.

## Hymenoptera

## Ichneumonidae

*Ophion* sp. (det. R. S. Peigler using I. D. Gauld & P. A. Mitchell, 1981, The taxonomy, distribution and host preferences of Indo-Papuan parasitic wasps of the subfamily Ophioninae (Hymenoptera: Ichneumonidae), Commonwealth Agric. Bur., Slough, 611 pp.). One reared from *Schinia* sp.

*Campoletis sonorensis* (Cameron). A few reared from 3rd instar *Schinia bina* and *S. chrysella*. White cocoons formed alongside dried host remains.

*Pristomerus spinator* (Fabricius). One reared from 2nd instar *Schinia bina*.

## Braconidae

*Cardiophiles abdominalis* (Cresson). Thirty parasitoids reared from *Schinia bina* and *S. arcigera*. Larvae of both host species were collected on *Aster spinosus* Benth.

*Microplitis croceipes* (Cresson). Two reared from larvae of *Schinia chrysella* collected on *Xanthocephalum dracunculoides* (DC) Shinnery.

*Cotesia marginiventris* (Cresson). From larvae of *Schinia chrysella* collected on *Xanthocephalum dracunculoides* we reared 58 parasitoids. From larvae of *Schinia bifascia* collected on *Ambrosia trifida* L. we reared 13 parasitoids.

*Meteorus* sp., probably *laphygmae* Viereck. One specimen reared from *Schinia* sp.

*Schinia* belongs to the same subfamily as *Heliothis virescens* (Fabricius) and *H. zea* (Boddie), two important agricultural pests. Entomologists working on *Heliothis* would be well advised to determine which species of *Schinia* occur in their region and at what population levels, since these could be significant alternate hosts for *Heliothis* parasitoids. Most of the parasitoids listed here attack *Heliothis* (Krombein et al., above).

We thank P. M. Marsh, C. W. Sabrosky, and R. W. Carlson (Systematic Entomology Laboratory, U.S. Department of Agriculture, Beltsville, Maryland) for identifying parasitoids. Robert Wyatt (University of Georgia, formerly Texas A&M University) identified hostplants. Roy O. Kendall kindly offered his previously unpublished records. Adult *Schinia* were determined by D. F. Hardwick (Biosystematics Research Institute, Agriculture Canada, Ottawa). Voucher specimens of parasitoids are in the National Museum of Natural History (Washington, D.C.) and Texas A&M University Entomology Department collections. Paper approved as TA-23149 by Director, Texas Agricultural Experiment Station.

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## BOOK REVIEWS

ANIMAL EVOLUTION IN CHANGING ENVIRONMENTS WITH SPECIAL REFERENCE TO ABNORMAL METAMORPHOSIS, by Ryuichi Matsuda. 1987. John Wiley & Sons, New York. 355 pp. \$44.95.

Truth *happens* to an idea. It *becomes* true, is *made* true by events. Its verity *is* in fact an event, a process: the process namely of its verifying itself, its verification. Its validity is the process of its validation.—William James, *The Varieties of Religious Experience* (1902)

What is truth? Specifically, what is truth in evolutionary biology? Neo-Darwinism remains constantly under attack; Fundamentalist Christians may be its most conspicuous antagonists, but neither Darwinism nor the neo-Darwinian synthesis has ever sat well among secular philosophers and humanists of various persuasions, and their objections to them surface and resurface periodically—the proverbial old wine in new bottles. The inheritance of acquired characteristics is an idea hallowed by time if not by recent consensus; it was a familiar theme in 19th- and early 20th-century lepidopterology, which in those days was at the frontier of evolutionary science. Its revival and embrace in Stalin's Soviet Union, with the concomitant suppression of Mendelian genetics for decades, added to its discredit elsewhere. But the idea of Lamarckian inheritance survives, and not only among nostalgic old Reds. It has a certain appeal to idealistic young radicals with no ties to Stalinism but with a faith in the perfectability of mankind through struggle, shared by old Lamarckists like Paul Kammerer. It also survives apart from politics among those who cannot accept an *undirected* ("random," but this word is always misused in such literature) process which leads to *adaptive* results. This position leads to some kind of vitalism. *Animal Evolution in Changing Environments* has links to the vitalist tradition. It is an exercise in wish-fulfillment: neo-Lamarckism *must* be true, therefore it *is*. Such declarations, alas, have no bearing on truth itself, only on our perception of what constitutes persuasive evidence pro or con. For lepidopterists this book is a window on an acrimonious argument which is an important part of our tradition, and is once again prominent in the broader sphere of evolutionary biology.

The book is in two parts. Part I is a polemic in favor of the notion that radical novelty in evolution is generated by genetic assimilation acting on components of the process of development, particularly on metamorphosis as expressed in stressful environments. Essentially the entire argument was advanced by Matsuda in an article in the *Canadian Journal of Zoology* in 1982, which can be seen as a précis of the book. It is summed up even more concisely by fig. 6 of the present volume (p. 244). Part I occupies the first 53 pages, concluding with a "proposal of pan-environmentalism": "Environment consists of both morphogenetic and selective factors . . . the former induces, by response of the genotype, variation upon which the selective factor(s) works . . ." and, graciously, "Neo-Darwinism may be retained as a method of analysis of the evolutionary process where the effect of environmental change or development is minor or negligible" (pp. 52-53). Part II occupies pages 57-355 and is a comprehensive and detailed bibliographic catalogue of cases of abnormal metamorphosis, neoteny, etc. judged by the author to be evolutionarily significant, arranged by taxa. (It also contains, in the aforementioned fig. 6 and accompanying text, the clearest statement of what the author's model *is*.) This is a remarkable achievement which would be of great value to theoreticians (who in these intellectually impoverished times in the English-speaking world know little comparative zoology as a rule)—if only they would read it. It does not read like a novel. It reads more like the telephone book. Matsuda is no Darwin or Gould or Dawkins, and the book suffers from disorganization and chopiness as well as a remarkably dull style for so fervent on advocate. And it must be read critically; like most compilers (the eccentric biogeographer Leon Croizat is a very good comparison), Matsuda himself accepts too much at face value and is prone to wish-fulfilling interpretation. As a student of genetic assimilation myself, however, I confess that about half of Matsuda's bibliography was new to me.

Because I have worked on phenotypic plasticity and genetic assimilation in butterflies

for some 20 years, Matsuda and I maintained a correspondence for some time which ultimately led to shared frustration. It was frustrating for Matsuda because he interpreted my results differently than I did, but was unable to convince me that he was right; it was frustrating for me because he seemed so plainly an enthusiast who was after verification of his ideas, which he equated with truth. (To be fair, clearly he saw me as unduly wedded to conventional neo-Darwinism.) More recently I had a somewhat similar interaction with Mae-Wan Ho, of Ho and Saunders, *Beyond Neo-Darwinism*; interestingly, Matsuda and Ho never did agree on the mechanism of genetic assimilation, although both professed a post-Darwinian, neo-Lamarckian viewpoint. A sociology-of-science approach to genetic assimilation as a problem has been undertaken by an American student, and his work should be forthcoming soon. It may clarify some of the issues, but its author has expressed the desire to avoid ideology as a factor. I think this is a mistake.

I am unhappy with Matsuda's handling of my own work and of butterfly polyphenism generally. This is no trivial matter. Historically, butterfly work informed and shaped the opinions not only of specialists like Standfuss and Fischer, but of generalizers and theoreticians who inspired much work and controversy—people like Kammerer, Weismann, Schmalhausen, and Goldschmidt, to name a very mixed bunch. I am especially unhappy because I think Matsuda was really on to something, and his premature declaration of victory will turn so many readers off that what is valid and important in this book will once again be relegated to oblivion. Matsuda, a morphologist by trade, had a fair grasp of both vertebrate and invertebrate endocrinology, but his model depends on his repeated invocation of "the mechanism of gene control," and this does not ring true. It is akin to the promiscuous use of similar language by paleontologists—macroevolutionists. One such, a friend of mine in fact, invoked "reverse transcriptase" in a seminar and was asked in all innocence by a paleontology grad student if he could explain what that was and how it worked; of course he could not. Neither could Matsuda, and he stopped short even of citing relevant literature, including references I gave him. Literature searching ended in 1983, but a lot of highly relevant stuff was already available by then. One searches in vain for the *real* quasi-Lamarckian literature here—exciting stuff such as Gorczynski and Steele on the immune system, John Campbell on gene automodulation, Spergel and others on heritable drug-induced metabolic defects and hormone problems, Cullis on genotrophy in flax—none of which would prove Matsuda's case, but which might at least render it more plausible. As it is, Matsuda clearly did not grasp this literature, and his death shortly before the book went to the publisher denied him the opportunity to make a case to impress any but the already-convinced.

Studies of wing-pattern modification in butterflies may or may not ultimately help to unravel the Lamarckian problem, but we may continue working with the knowledge that this book does not close the matter. Perhaps someday someone will be able to make the assertions Matsuda made in this book, and back them up with a solid case rather than a lot of arm-waving. Then and only then will truth "happen to" the neo-Lamarckian idea.

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THE BUTTERFLY GARDEN, by Mathew Tekulsky, introd. by Robert Michael Pyle, illus. by Susanah Brown. 1985. Harvard Common Press, Boston. x + 144 pp. \$8.95 (paper), \$16.95 (cloth).

THE BUTTERFLY GARDENER, by Miriam Rothschild and Clive Farrell, illus. by Elisabeth Luard. 1983. Michael Joseph Ltd. and Rainbird Publishing Group Ltd., London. 128 pp. UK £7.95 (hardbound).

When L. Hugh Newman and Moira Savonius published their classic book *Create a Butterfly Garden* in 1967 (John Baker, London), they crystallized and explored for the first time the theory of gardening to encourage butterflies. Native butterflies must be tempted into gardens by their favorite nectar flowers, they asserted, and some may establish breeding populations in gardens if the proper larval foodplants are grown.

Occasional articles on the subject have since been published in horticultural, lepidopterological, and environmental journals, but Rothschild and Farrell's *The Butterfly Gardener* and Tekulsky's *The Butterfly Garden* are the first book-length treatments of this special type of horticulture to appear in almost 20 years. Both are welcome, helpful additions to the limited and scattered literature on butterfly gardening.

*The Butterfly Gardener* is a strange marriage of what might better have been two separate volumes. The first part, "The Outdoor Butterfly Gardener," is by Miriam Rothschild of the renowned family of British naturalists (daughter of Charles, niece of Walter), an eminent, even awesome entomologist, naturalist, and conservationist in her own right. The second part, "The Indoor Butterfly Gardener," is by Clive Farrell who designed and established the famous London Butterfly House at Syon Park. Rothschild further treats the theme begun by Newman and Savonius, while Farrell explores a very different subject—the butterfly zoo, wherein breeding populations of tropical butterflies are maintained inside a special greenhouse containing their caterpillar hostplants and nectar flowers.

"Flowers and insects have travelled down the ages together, bound up in a kaleidoscopic rainbow relationship of mutual benefit and mutual exploitation," writes Rothschild. Her large garden is divided into three sections, a stone-walled kitchen garden, the grounds surrounding the house and courtyard, and an acre of flowering hayfield in which she has established more than 100 species of wild plants. Her seasonal approach is practical, emphasizing cultivation, conservation, and management of grasses, shrubs, and wildflowers that serve as larval foodplants and adult nectar sources for butterflies. The book includes directions for gathering and sowing wildflower seeds, techniques for mowing fields to minimize disturbance to butterflies in all life stages, and a butterfly garden design. Likewise, much useful information on British butterflies is enmeshed in anecdotes and in historical, cultural, and literary allusions that are a pleasure to wander through, just like a butterfly-filled garden itself. Her chapter on "Grass" is one of the most original, inspired, and delightful short essays I have read. The book deals less with butterflies and gardening than with the author's unique appreciation of them. Her wit and erudition, child-like curiosity, sensitivity, and humility, as well as her love of gardens, plants, butterflies, and people and her understanding of how they interact, shine in every line. This is a piece of great literature. Like Carl Sagan, she is able to distill the spirit of her subject in popular prose.

Farrell's chapters detail the indoor culture of exotic butterflies and their foodplants as a display for public education and enjoyment. Warmth, light, humidity, and ventilation are important considerations in a greenhouse managed for insects as well as plants. Also, an enclosure of this type must be very tight to prevent escape of butterflies and entry of parasites and predators, and no pesticides can be used. In richly informative, straightforward prose, Farrell treats each aspect of indoor butterfly culture, concentrating on easily reared tropical species. His level of detail is thoughtful, helpful, and indicates vast experience and a real talent to communicate. His directions for breeding captive butterflies are among the best available. Farrell's contribution is unique in the literature.

Mathew Tekulsky's *The Butterfly Garden* is the first comprehensive textbook on the subject, and the first butterfly gardening book slanted to the United States and Canada. The author basically reviews existing butterfly gardening lore, giving detailed abstracts of longer original treatments. He includes three chapters on garden setup and plants, plus information on feeders for butterflies like those for hummingbirds, hibernation boxes for adult angling butterflies, bait traps, and educational activities for the butterfly garden. Although the author lives in California, he included examples of plants and butterflies from all parts of the continent north of Mexico. Tekulsky is an excellent writer (his chapter transitions are especially well done), but I have a vague sense of disappointment at the

lack of original material. Even so, I expect the book to become a classic because it is so thorough. It proved a useful text for a butterfly gardening class I taught in 1987.

Both books are well illustrated. Rothschild and Farrell's has eight exquisite color photographs by Kazuo Unno, Carl Wallace, and Tony Evans, a color dust jacket, and 21 pen-and-ink drawings and decorations by Elisabeth Luard. Tekulsky's has 43 lovely pencil drawings and a beautiful color cover by Susanah Brown. Luard's designs are often very fine (especially the frontispiece), and her drawings do successfully communicate concepts, but poor technique frequently shows in an irritating overuse of stipple-dots. Brown's pencil drawings are wonderful. Both artists have depicted plants and butterflies in lifelike poses.

Each book contains appendices on garden butterflies; wild and cultivated nectar flowers; commercial sources of seeds, plants, butterflies, and equipment; organizations and publications dealing with horticulture, Lepidoptera, wildflowers, and conservation; and references. Tekulsky's section on "Further Reading" is the most complete bibliography of the subject I have seen. The appendices are the most practical sections of the works.

For those who derive great pleasure from seeing the living, moving color of wild butterflies among their blooms, these books are a must!

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SPHINGIDAE MUNDI. Hawk Moths of the World, by Bernard D'Abrera. E. W. Classey, Faringdon, England. 226 pp. 79 plates. 250 × 340 mm, hard cover. £97.50 (ca. \$145.00).

Somebody once remarked to Dr. O. Niemeyer, the architect who designed most of the government buildings in Brasilia, the modern capital of Brazil, "your architecture is beautiful, but not always functional". Niemeyer kindly replied: "beauty *is* a function". D'Abrera's book *is* a beautiful book, and, in Dr. Niemeyer's concept, this book fulfills that function perfectly. It is artistically designed, and the plates are magnificent. The colors of specimens, especially those of Neotropical species, are well-balanced. Except for species represented by old, faded, and descaled specimens, the creatures would not be ashamed of their portraits.

To help the reader understand viewpoints to follow, we provide some background information. The first author met D'Abrera in 1979 at the British Museum (Natural History). They frequently spent long hours discussing work, dreams, and difficulties. D'Abrera does not regard himself a professional entomologist. He is, above all, an artist whose main interest is to express his talents through butterflies and moths, and at the same time to produce something beautiful and useful to others. Also, he is not supported by taxpayers, so has to work under great pressures, especially economic pressures. It is difficult to write books on butterflies and moths for a livelihood and to finance publication. This includes the cost of travelling more than 12,000 miles (19,300 km) from his home to the British Museum (Natural History), where he has to do his work, and production financing which includes preparing plates, writing text, designing, type setting, color separation, printing and binding, and export!

We offer this background for several reasons. First, it is important to recognize the motivation and personal sacrifice behind D'Abrera's books. Second, previous reviews of D'Abrera's books may have been unfair. We do not deny there are mistakes, but are they solely the author's fault, or do they reflect the chaotic state of lepidopteran taxonomy? D'Abrera clearly says that the main objective of this book "... is to provide, in a synoptic form, a modern illustrated systematic list of the known species of the Hawk Moths



(Sphingidae) of the World. It is not a revision." Is it the responsibility of authors who produce such books to solve all the taxonomic problems before publishing something useful? The task would take many years and involve many workers. Finally, it is possible that some previous reviewers did not, or did not try to, understand the audience to which D'Abrera's books are directed. Professional entomologists might feel that D'Abrera's books only add to the confusion already accumulated. But, what about the people who do not have access to good collections, who cannot travel to museums around the world to examine material, who do not have access to an extensive library? Should they wait another century until the taxonomic chaos is sorted out? In this case, it is preferable to have his work with errors than nothing at all.

This book is divided into four sections: introduction, text and plates, bibliography, and index. The introduction consists of a Foreword explaining objectives, conditions under which the work was carried out, and the style followed throughout. It is followed by an Acknowledgements section expressing gratitude to the late Alan Hayes. The book is based on a check list prepared by Hayes, and on the collection he curated for more than 20 years at the British Museum (Natural History). The Introduction is elegantly written, and describes previous works and general sphingid biology. A useful two-page section entitled "Notes for the Guidance of the Reader" explains abbreviations and symbols used in text and plates, and includes three figures showing important features of wings, pretarsal joint, and head. A Systematic Catalogue of Genera, listing genera in the same order as the text, ends the introduction.

The body of the book—the text and plates—is organized practically. The book was designed to present text alternating with plates so that when the book is opened, text is on the left-hand side, and figures are on the opposite page. This allows the reader to consult the book without having to turn pages back and forth to compare text and figures. This format could not be followed consistently, however, because when many small specimens are on a plate, the accompanying text cannot be included on a single page. The text provides useful information such as variation in color patterns, diagnostic characters, and larval host plants. The plates show entire moths in actual size, and in several cases the underside is also shown to distinguish similar species. The Appendix consists of 4 plates which illustrate 39 type specimens of species not represented in the British Museum (Natural History). They vary in quality: some are good; others are poor, but useful, since most have never been figured. Selected References omits some important works such as M. Draudt (1931. In A. Seitz, *Macrolepidoptera of the World*); W. Rothschild & K. Jordan (1907. *Genera Insectorum*); and H. Wagner (1913–1919. *Lepidopterorum Catalogus*). Finally, there are two indexes, one for genera and one for species.

This book has long been needed. The last comprehensive treatment of Neotropical Sphingidae was that of Draudt (cited above). D'Abrera recognizes approximately 1050 species, and illustrates more than 1000. Draudt listed only around 480 names and figured 260 Neotropical specimens. Further, Draudt's work had many faults, specifically with regard to combinations, that are corrected in D'Abrera's book. But we disagree with the sinking of *Neococytius*, and the transfer of *N. cluentius* to *Cocytius*; several cases pointed out by D'Abrera, such as *Dolba* and *Dolbogene*, should have been synonymized following the same criteria. D'Abrera himself regards the latter differences as "trivial." It would have been better to use the same criteria throughout, or to leave genera alone.

The Neotropical species were checked, and no misidentifications found. However, the book has a few mistakes that should have been corrected by the editorial panel. The most serious is authorship and date of family Sphingidae, which is actually Latreille 1802, not Samouelle 1819; and the nominate subfamily name should bear the same authorship and date. Other mistakes include incongruences between numbers of species given by the author and numbers treated in genera. For example, under *Paonias* it is stated that there are two species, but three are actually treated. The same occurs with *Hemeroplanes*, where the numbers are four and five, respectively. In the plates, *Callionima neivai* and *Eumorpha adamsi* are identified as "*neavei*" and "*damasi*." A figure of *Protaleuron rhodogaster* is stated to be in the Appendix, but no figure was found.

By examining this book, it becomes evident that Sphingidae are in desperate need of a revision of higher classification. Several groups such as *Xylophanes*, *Theretra* and



*Cechena* have species that are difficult to tell apart superficially but are kept in separate genera because they occur in different faunistic regions. Because the groups were too large, or because of difficulties in communication, each fauna was studied separately. The result is that each faunistic region has an independent set of genera. It would be useful to subject the genera to a rigorous character analysis. Cladists, here is a good subject to study!

D'Abrera did a good job on this book. For those who want to start or to organize a collection, and to study the group, it is a good starting reference. We recognize that for many who live in the Poor World, £97.50 is a lot of money. However, when we consider the quality of this book, the prices of books of lesser quality, and the fact that this is a book one would buy only once in a lifetime, it is a bargain.

We thank R. W. Hodges for critically commenting on the review.

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G. Wykes



30 August 1988

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**Cover illustration:** Male walnut sphinx, *Laothoe juglandis* (J. E. Smith), in a typical day resting posture (1½ life size). Submitted by Gerald P. Wykes, 2569 Reinhardt Road, Monroe, Michigan 48161.



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## CYRIL FRANKLIN DOS PASSOS (1887-1986)

RONALD S. WILKINSON

228 Ninth Street, N.E., Washington, D.C. 20002

Cyril Franklin dos Passos, eminent student of Nearctic Rhopalocera, and a Charter and Honorary Life Member of the Lepidopterists' Society, died on 29 October 1986, only a few months before he would have celebrated his 100th birthday.

Many who are aware of Cyril's entomological contributions may not know that during an extraordinarily long and full life he had two quite distinct and successive careers. The second is of more concern to us, but as Cyril did not begin his work on butterflies until he was past the age of 40, something must be said of the first.

Cyril was always aware of the Portuguese heritage of his family, a fact that this writer recalls most vividly because of the excellent Madeiran wines served at the dos Passos table. Cyril's paternal grandfather Manoel (later Manuel) dos Passos emigrated to the United States from Ponta do Sol, Madeira, in 1830, becoming a cobbler and later a shoemaker, and finally settling in Philadelphia where he married Lucinda Cattell. There were six children, including Cyril's father Benjamin Franklin Dos Passos (the American family had capitalized the Portuguese lower case d) and an older brother, John Randolph, who would also be of considerable importance in Cyril's life.

John Randolph studied law and became an eminent and affluent New York City attorney, specializing in brokerage and corporation law. He defended trusts, opposed regulation of business by government, and wrote extensively on these and other subjects. He took Benjamin Franklin into his law firm, which became Dos Passos Brothers. Cyril, an only child, was born in New York on 7 February 1887. His mother, Isabel Kirker Strong, was of English descent. His father died in 1898 when Cyril was eleven.

By his own account of his education, Cyril attended several private

schools, finally spending eight years at Cutler School in New York City, and graduating in 1905. He read law for two years at Dos Passos Brothers, and entered New York Law School in 1907. Cyril attended classes while working half days in his uncle's Broad Street offices. After receiving his LL. B. *cum laude* in 1909, he was admitted to the New York bar and began to practice in the family firm, becoming a partner.

John Randolph Dos Passos represented railroad interests, and played a large part in the reorganization of various lines. His protégé Cyril eventually entered the railroad business, becoming president and a director of the Kansas, Oklahoma & Gulf Railway Company, which ran from Joplin, Missouri, to Denison, Texas. When a competing line forced Cyril's company into receivership, he incorporated and became secretary, treasurer, and later president of a brokerage firm, the New York and Hanseatic Corporation. During these business activities Cyril maintained his place in the law firm. When John Randolph died in 1917, Cyril inherited the "good will, name and business of Dos Passos Brothers" and his uncle's extensive law library. He was, however, Cyril *dos* Passos, because his mother had encouraged him to use the Portuguese form. (Despite an interest in his own Portuguese heritage, John Randolph's son and Cyril's cousin, the well-known literary figure John Roderigo Dos Passos, chose to retain the Americanized capitalization.)

On 3 August 1927 Cyril married Viola Harriet Van Hise, who would direct his interests toward entomology. She was the youngest daughter of Anthony H. Van Hise and Harriet Louise Archer, and was born at Newark, New Jersey, on 24 November 1891. Having earned a comfortable fortune, Cyril was able in 1928 to retire from law and business, and devote his time to leisure pursuits. The couple lived in Ridgewood, New Jersey, for several years, and enjoyed their summers at the Rangeley, Maine "camp" which Cyril had built before the marriage for hunting, fishing, and other recreation. Their son Manuel, who survives him, was born on 4 February 1929.

Thus was the stage set for Cyril dos Passos' second career. In later life he enjoyed telling the story of his discussions with Viola about taking up an instructive and useful pursuit. Cyril suggested art. Viola, who had been reading copies of W. J. Holland's butterfly and moth books, voted for entomology. She won the day. They decided that she would collect and study Nearctic moths, and he would devote his attention to butterflies.

Collecting began in earnest at the Rangeley camp in 1929. The two set out a sugaring trail, a line of Rummel bait traps, and eventually had a large light trap constructed. A neighbor suggested that Cyril visit the Department of Entomology of the American Museum of Natural History (AMNH), and he did so, making the friendship of Frank E.





Cyril F. dos Passos and friend at Quimby Pond Camps, Rangeley, Maine, 1973

Watson, who helped identify his and Viola's captures. Cyril assisted Watson in disinfecting and otherwise caring for the AMNH collection, and was soon an unofficial "regular," enjoying the encouragement of the department curator, Frank E. Lutz.

Meanwhile, planning was under way for the magnificent French Provincial house which would become well known to Cyril's scientific friends. He had always been partial to things French; his mother (who spoke French fluently and had a French maid) had taken him to France a number of times. Ideas for the house and grounds were assembled

from books on minor chateaux and turned over to an architect. Construction began in spring 1931 on ninety partially wooded acres in Mendham, New Jersey. Cyril and Viola wished to move in at the earliest opportunity, and were able to do so by winter.

At the Mendham "chateau" part of the second story was devoted to specimen storage and a rapidly growing entomological library. Viola placed her moths in traditional cabinets, separated by a partition from Cyril's collection. He adopted the use of Watson-Comstock store boxes, designed by his AMNH friends Watson and William P. Comstock, and constructed at Cyril's expense by the museum carpenter. Cyril described the box in his 1957 obituary of Comstock as "quite an ingenious, light and inexpensive affair with top and bottom of heavy cardboard and sides of wood. The bottom is lined with pressed cork." As the collections grew, Viola's moths were moved to another spacious room, and Cyril's specimens filled the original area.

His earliest entomological publications were undertaken with a young correspondent and collecting companion, L. Paul Grey, who has contributed a memoir of his own to this *Journal* issue. The 1934 dos Passos-Grey annotated list of Maine butterflies and its supplement were natural beginnings for the initially Maine-oriented pair who would later revise the Nearctic "argynnis." Cyril gradually became a respected taxonomist, but during his career also published investigations of life histories of imperfectly known butterflies. He was an avid field collector, and because of his financial resources was able to augment his own efforts greatly by hiring collectors to work for him in some remote areas. For example, the first of his many papers with descriptions of new subspecies was based on material sent to him from Newfoundland by Hugh McIsaac.

In 1936 Cyril was appointed Research Associate in the Department of Entomology, AMNH, through Lutz's recommendation. The appointment was regularly renewed until the year before Cyril's death, so that he served a full half-century on the scientific staff. He was instrumental in acquiring the first really large collection of North American butterflies to be added to the AMNH's then relatively modest holdings, being a substantial contributor to the purchase of Jeane D. Gunder's 27,000 specimens in 1937. Cyril later published a catalogue of the Gunder types; he also obtained Gunder's library and added it to his own. As time passed, Cyril was able to buy a number of established collections of significance and integrate them into his previous holdings. One of his purchases was the Alberta and Illinois material of Thomas E. Bean, a correspondent of William Henry Edwards who supplied considerable data used in the third volume of *The Butterflies of North America*; among others were the collections of Max Rothke, E. H. Blackmore, R. F. Sternitzky, Owen Bryant and Louis Doerfel. Types went to AMNH,

although Cyril retained most paratypes. When his purchases included moths, these were placed in Viola's cabinets.

Cyril's concern about the significance of types led him to devise an improved method of photographing type specimens and their labels. An apparatus for the purpose had been described by Gunder in 1930, but it had defects, which Cyril remedied. His folding device, utilizing a Leica Model F camera and adjustable floodlights, could adequately record the insect and the many labels often found on types, and could be placed in a suitcase for travel. Cyril visited American and European museums with his camera, and although he restricted his activities chiefly to recording types of North American Rhopalocera, he hoped that through cooperation all remaining type specimens of Lepidoptera could be photographed; while many types might be lost to science over the years, Cyril argued that photographs would create a record that could last indefinitely. By 1945, when he published a description of his apparatus, he had recorded as many as 1200 types. The project was continued, and Cyril's photographs are now in AMNH. Some have been reproduced in his own papers and those of other workers. His original idea still has merit.

Cyril's early taxonomic work chiefly concerned Lycaenidae and Satyridae, although he also published on nymphalids. His first synonymic catalogue, which appeared in 1939, was of the North American Satyridae, part of a proposed but ill-fated catalogue with references to original descriptions of all Rhopalocera north of the Mexican border, edited by F. Martin Brown and R. W. L. Potts, which failed from lack of funding.

During World War II Cyril suffered a great loss. Viola, who had continued to collect moths, had a heart attack in 1939, and her activities were restricted. She died at Rangeley on 29 August 1944. Later in that year Cyril donated her collection, which included over 12,000 specimens, to AMNH.

The collaboration with L. Paul Grey on the Argynninae, discussed in the accompanying memoir, began to bear fruit during the war years. Their first three joint papers appeared in 1942 and 1945; the third was one of three independent genitalic studies (the others by B. C. S. Warren and F. A. T. Reuss) which led to a new scheme of classification of the subfamily, restricting the genera *Argynnis* and *Brenthis* to the Palearctic region, leaving *Boloria* as Holarctic, and *Speyeria* and *Euptoieta* as Nearctic genera. The dos Passos-Grey systematic catalogue of *Speyeria* was published in 1947. They concluded that although 109 published names attributable to *Speyeria* were valid, only 13 species were involved.

Reviewing the revision in *The Lepidopterists' News*, Charles L.

Remington noted that before the work of dos Passos and Grey, "different authors accepted a widely varying number of distinct species in the group, many supposed affinities were entirely wrong, and uncorrelated new 'races' continued to be described. The challenge of ordering the chaos was grasped at that time by L. Paul Grey, who disposed of his excellent collection of North American Lepidoptera to devote all his time and space to the 'Args.' He was fortunate to be joined by C. F. dos Passos, who had the means, the equipment, and the methodical mind to scour the scattered literature, visit a number of museums to examine carefully the types, and study the numerous nomenclatorial problems." The 1947 paper has recently been mentioned by Scott in *The Butterflies of North America* (1986) as helping to turn the trend of "splitting" into the more sophisticated concept of species we have today.

When the Lepidopterists' Society was formally constituted in May 1947, Cyril was a charter member. He served on the very early Board of Specialists (which identified specimens for Society members) for the family Satyridae. For the first two and a half years of its existence the Society operated under "articles of organization," published in the first issue of *The Lepidopterists' News*. In 1950 editor Remington asked Cyril to prepare a formal constitution and by-laws. He did so, and served as chairman of an international committee to study and approve the draft, which was ratified by members at the first annual meeting. Cyril's committee appointed temporary officers to serve the Society until the first election by the membership, and it was due to the dos Passos committee's good judgment that the Society's first president was a lepidopterist of the very highest reputation, Cyril's friend James H. McDunnough, whom he had met while photographing types at the Canadian National Collection in the 1930's. Cyril served on the Karl Jordan Medal Awards Committee, and was elected an Honorary Life Member in 1973.

He attended the International Congresses of Zoology at Paris (1948), Copenhagen (1953), and London (1958), participating in the prior colloquia, sections, and other activities devoted to nomenclature. He read papers on nomenclature at Copenhagen and London, and frequently during the decade (as well as occasionally afterwards) contributed to the *Bulletin of Zoological Nomenclature*, proposing and commenting on decisions of the International Commission, and discussing and suggesting amendments to the *Règles Internationales*, later the *International Code of Zoological Nomenclature*. He also traveled to a number of International Congresses of Entomology, and during these and other journeys out of the country, he made many scientific friendships and

added considerable material to his entomological holdings. He especially enjoyed collecting in Europe, and did so widely.

During this active period, Cyril was appointed Research Associate by the Carnegie Museum (1952). He continued to publish on Satyridae and on topics as diverse as the eye colors of *Colias* and the ethics of scientific criticism. On 3 September 1959, Cyril married Maria Amália Pita Pestana Reis, who survives him. She is the daughter of Maria Pita de Macedo and Miguel Pestana dos Reis and was born in Ponta do Sol, the birthplace of Cyril's paternal grandfather. Maria Amália brought Cyril much happiness, and the great success of his second marriage was evident to his friends.

The result of a project of some years' length appeared in 1964 as *A Synonymic List of the Nearctic Rhopalocera*, this Society's Memoir No. 1 and, with its supplements, Cyril's most significant and useful contribution as single author. Much of his time in later years was devoted to the full catalogue of Nearctic butterflies announced as forthcoming in the introduction to his 1964 checklist. The typescript eventually grew to seven volumes, but the work was discontinued due to the impending appearance of Miller and Brown's *A Catalogue/Checklist of the Butterflies of America North of Mexico* (1981).

Work on such tasks as the checklist and catalogue was made easier because Cyril had built one of the most extensive private entomological libraries in America. When he wished to search the literature he seldom had to leave his home, for most of the works in which North American butterflies were described, from the 18th century onward, were there, not only monographs but runs of journals. For an historian and bibliographer of entomology, the most exciting part of a visit to the dos Passos chateau was the time spent in the library. One example will suffice; during research on John Abbot, I was examining varying watermarks in copies of Smith and Abbot's *The Natural History of the Rarer Lepidopterous Insects of Georgia* (1797) to determine the length of its publishing history. Cyril was able to show me not one copy but two, the second being a volume of the plates issued later with a publisher's imprint I have never seen elsewhere than in the great library which was donated to Wittenberg University, Springfield, Ohio, during Cyril's last years.

His concern with books and libraries, and his devotion to AMNH led Cyril to give considerable assistance to the Museum's library. He published a number of bibliographical papers and (with William D. Field and John H. Masters) a very useful volume, *A Bibliography of the Catalogs, Lists, Faunal and Other Papers on the Butterflies of North America North of Mexico Arranged by State and Province* (1974).



Some of Cyril's bibliographical writings dealt with the actual dates of publication of literature containing descriptions of insects, which of course are important in determining priority. Cyril's frequent work with descriptions quite naturally led to an interest in the history of entomology, to which his major contribution was his edition of William Henry Edwards' entomological reminiscences (1951); the manuscript was loaned to him for the purpose by Edwards' granddaughter.

Among Cyril's later publications were two substantial studies (and models for emulation) co-authored with Alexander B. Klots. The first (1969) concerned the pierid *Anthocharis midea* (Hübner). As explained in their introduction, for many years they had recognized the need for a detailed investigation of *midea* to clarify such problems as geographic variation and nomenclature, and had been accumulating data and specimens toward that end. The resulting paper, which also treated life history, foodplants, and parasites, was an exemplary discussion of a species and its subspecies. They had also been gathering data about the lycaenid *Erora laeta* (W. H. Edwards), and had jointly and severally conducted field studies between 1934 and 1968. Their thorough paper on the genus *Erora* (1982) examined early stages, ethology, ecology, and geographic distribution of *laeta* and *E. quaderna sanfordi* dos Passos, and provided synonymies. An extensive taxonomic study of the satyrids *Lethe portlandia* (Fabricius) and *L. anthedon* (Clark) was published by J. Richard Heitzman and Cyril (1974); incidentally, these three papers provide excellent examples of the use of Cyril's photographs of type specimens. On his own, Cyril produced his usual variety of publications nearly to the end, although his last appearance in print was as co-author with Clifford D. Ferris, James A. Ebner, and J. Donald Lafontaine of an annotated list of Yukon butterflies (1983). It was appropriate that Cyril's final paper concerned the far-northern fauna he loved.

Cyril donated his entomological collection to AMNH in 1980. At that time the butterflies were contained in over 1250 store boxes. Announcing the event in the *Journal*, curator Frederick H. Rindge stated that the collection was undoubtedly "the single largest and most complete one of North American butterflies ever made by one individual." He noted that the gift included over 65,000 specimens; of those which were mounted and identified, 57,870 were North American and 6182 were European. There were 464 paratypes (Cyril had consistently deposited holotypes and allotypes in AMNH) and 617 slides, chiefly of genitalia but also of venation. Cyril intended that his correspondence and other manuscript materials should go to AMNH, and the transfer was made by Maria Amália in 1987.

Cyril was a member of a number of scientific societies, and a Fellow

of the Royal Entomological Society of London (1950–). He was also a Fellow of the Linnean Society of London (1977–), where many years previously he had photographed Linnaeus' types of North American butterflies. Wittenberg University awarded him an honorary D.Sc. in 1965, and McDunnough named the copper *Lycaena epixanthe dospassosi* after him in 1940.

Those who knew Cyril were aware that his interests were by no means limited to entomology. They ranged over the entire field of natural history, including ornithology, geology and paleontology, and extended to archaeology. He assembled extensive and valuable holdings of classic postage stamps and covers of the United States, including proofs, and also acquired the stamps of Nepal, Tibet, Heligoland, the British Commonwealth, and France. He was a contributor to philatelic journals.

Cyril was a man of many parts. He gave to entomology an unrivaled private collection of Nearctic Rhopalocera, many examples of financial generosity, and 50 years of publications of high professional quality. Much has been written by historians about the professionalization of science, a relatively recent transition from a past in which scientific foundations were laid by workers educated in other areas. In some cases the process has led to too rigid a distinction between professional and amateur. It is still possible to make important and lasting contributions to entomology without earning a graduate degree in the subject or a related discipline; witness Cyril F. dos Passos, an amateur who made our science his profession and served it very well.

## MEMORIES OF CYRIL F. DOS PASSOS (1887-1986)

LIONEL PAUL GREY

Rte. 1, Box 1925, Lincoln, Maine 04457

The magnitude of "d.P.'s" accomplishments, as chronicled in the preceding article by R. S. Wilkinson, will attest that he was an unusual individual. Some of my memories of him, and experiences with him as a correspondent, collaborator and friend, perhaps will add to the picture of the kind of person who could live so full a life, with outstanding success in so many varied endeavors.

Quite inevitably he had to be an energetic worker, but in addition he carried methodical procedure and time budgeting almost to the status of an art form. When he was in his prime, few if any random intrusions crept into schedules determined days or weeks in advance. Usually there was a brief nap after lunch, followed by a half-hour's walk; aside from this, very little else in the way of relaxation except at meals. Those were ceremonious, especially at dinner, and served at the precise times appointed. He had uncompromising ideas about how things should be done, including the conduct of his own life and the running of his household. When you dined with him you wore a coat and tie. I used to describe him (jokingly, and never within his hearing) as "the last of the barons". Indeed he was more the Old World aristocrat (in the best sense) than the American businessman.

My first contact with him came shortly after he had begun studies at the American Museum. He wrote to me for information on collecting Maine butterflies. I learned that he had a summer camp at Rangeley, where he came to escape his perennial troubles with hay fever. This led to meetings, discussions, and the beginning of a lifelong friendship. Our first meeting probably left a lingering impression, to put it delicately, since I was on a manure cart at the time, spreading richness on my father's farm. Anyhow, he never forgot that I was his "very first entomological correspondent", and he came to be my closest associate among the amateur lepidopterists who, at that time, in the very early 30's, comprised a rather small fraternity.

On one of our earlier outings we collected *Oeneis katahdin* Newcomb. Cyril had reserved a cabin for us at a sporting camp on Daicey Pond, reached by a long hike from where we had to leave the car. The next day we paddled across the lake and struck out through the woods with only occasional glimpses of the distant mountain. The region then was almost as wild as in Thoreau's time, with few trails. We finally came out in a clearing where a major campground of Baxter State Park now is located; here we picked up Katahdin Stream which we followed

up to the steep slopes of the spruce belt, and from thence to timberline and up over the rocks to the tableland. I still remember how amazed I was that a city lawyer could find his way through the woods as well as a country native, and could endure the long day's ordeal without apparent discomfort. Worse yet, he caught more *katahdin* than I did, using the slow stalking approach while I was dashing hither and yon making wild swoops at anything arising from the tundra. Even the day's end had a lesson for me, when, in the evening back at our cabin, he spent a few minutes writing in a diary, advising me to consider the uses of such. For him, in future years, there would be no doubt concerning what he had accomplished during this particular day of his life, nor would there be any lack of details should he ever wish to refresh his memory about his series of *katahdin* butterflies and the place where he took them.

Subsequent occasions bore out the conclusion that Cyril was a tough physical specimen, which never would have been guessed in view of his small stature and rather delicate frame. But then, this seems to have been a family heritage, judging from stories told of his cousin, John, the well-known author. Apparently the latter had lead a wild life, soaking up "local color" in some of the most dangerous places on earth, a midget holding his own among giants. As one commentator put it, "John actually did the things Hemingway bragged about doing". This was a clue and key to much of Cyril's success and also to a reputation he gained at the Museum of being difficult to get along with, namely, the trait which psychologists term "overcompensation". He always was aggressive when challenged.

In retrospect I marvel that we remained friendly, since I ventured to argue with him rather hotly on various issues. Predictably, he was laissez-faire capitalist in philosophy, often in a rage against the socialist trends of the day. In view of our present national debts and deficits I am becoming convinced that his opinions made far more sense than mine.

Certainly our entomological relations always were very cordial. A mountain of correspondence passed between us as we worked out details of a major joint project, a study of nearctic "*Argynnis*". This was for several years a shared labor, with results which at that time proved to be somewhat controversial. As Scott has pointed out, in the latest *Butterflies of North America*, we made a break in tradition toward synthesis, away from the (European-fueled) tendency to finer and finer splitting. Cyril's role in all of this sometimes has been underestimated. He was in every respect the senior author. He did a lion's share of the work and definitely was the "maker-possible" for my contributions. A bit of review may be of historical interest:

I can pinpoint the exact moment when this project was born. It was sparked by our shared exasperation that nobody seemed able to identify our western material, and ignited one day when Cyril was showing me some California specimens which he had purchased with the understanding that they were to have been identified by the collector. But they arrived minus names, aside from one specimen which bore a label stating "this looks like an oddball". So it did, and to our eyes so did all the rest.

From that time onward we each began a serious study of those enigmas, Cyril working with the literature and with the problems of nomenclature hinging on locating and identifying type materials, while I accumulated specimens and solicited all my collector friends for locality data. Apparently we each had intuitively analyzed our respective strengths and adapted to integrate them. He trusted and never questioned my developing ideas concerning the speciations, while I certainly was in no position to question his grasp of the literature or his plans for organizing our subjects. It made for a smooth-working partnership.

Wilkinson has noted some of the instances of Cyril's quiet philanthropies. I suspect Cyril derived considerable enjoyment in introducing me to the world beyond my native turf. He paid my way for trips to Boston, New York, Philadelphia and Pittsburgh, where I expanded our argynnid data and was able to see numerous types. An incidental but priceless feature of those journeys was the opportunity to meet and talk with people such as Andrei Avinoff at Pittsburgh, Vladimir Nabokov and Nathan Banks at the Museum of Comparative Zoology, and of course the entomologists then at the American Museum, including Lutz, Mitchener, Klots, and that very gracious gentleman, W. P. Comstock. Also, Cyril took me to meetings where I heard lectures by such legendary figures as "William T. Davis of Staten Island" (the two are inseparable) and Robert Cushman Murphy, the great authority on oceanic birds. All in all, quite an education for a youth from the backwoods! These debts are gratefully acknowledged.

Also, I should express my appreciation for his cautious guidance as we came nearer to our goal of revising the North American argynnids. It had become apparent fairly early that the records seldom indicated more than 6 or 8 distinct kinds of populations of those butterflies in any single general area, a fact of significance when compared against the listings then current, which ran to 100 "species" or more. Collations of local data sets also indicated numerous instances of intergrading. I felt that we were on the verge of solving the puzzle, but Cyril then urged that we had a duty to enlarge the perspective to include whatever might appear when native argynnids were compared with those on the other continents. A fairly comprehensive genitalic survey of the Nearc-



tic species had been completed, but the task of studying the world argynnines was slowed by difficulties in procuring the needed material.

Thus, it was 1947 before our Systematic Catalogue of *Speyeria* finally was published. A few corrections have been required, both to Cyril's nomenclatorial and other data and to my concepts of the speciations, but these have been gratifyingly few considering the tangle we were dealing with. It was, indeed, as Scott has noted, a turning point in the philosophy of butterfly "species", but unfortunately we were too much captives of the times to have broken loose from the addiction to "sub-species". In fact, back at that time it would have been unwise to have reduced the number of such taxa, even though many are hardly more than unstable local color forms. As Cyril had warned me, we encountered considerable resistance to our radically altered classification, the big difficulty lying with our downgrading of many taxa traditionally hallowed as "species". To help soften those outrages to custom we thought it essential to retain numerous subspecific names and even to propose some new ones for the same purpose of indicating some of the connecting links and the widespread continuity of intergrading within the series discriminated as constituting polytypic species.

After those prolonged associations it seemed only natural that we should remain close and affectionate friends. When failing health forced him to curtail his entomological activities he presented me with the entire contents of his laboratory. I remain surrounded by reminders of his kindness.

In closing, it seems fitting to recall one of Cyril's most striking mannerisms. He never lingered when the time came to part—a wave of the hand, a "bye-bye" and he would turn abruptly and walk away. Fond recollections remain.

ANNOTATED BIBLIOGRAPHY OF THE  
ENTOMOLOGICAL PUBLICATIONS OF  
CYRIL F. DOS PASSOS (1887-1986)

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This bibliography includes all of Cyril dos Passos' entomological publications known to me except his abstracts of current literature published in early issues of *The Lepidopterists' News*. All publications have been personally examined; in most cases separates or reprints had been furnished to me by the author during his lifetime with a bibliography in mind, and a search of the literature has revealed additional publications.

Arrangement of entries is chronological according to actual dates of publication, which were determined by examination of journal issues, and through correspondence and other methods. Items identified by asterisk (\*) have not been dated precisely, but these do not affect the chronology. Titles of publications are exact, although I have uniformly italicized generic and specific names. Citations of place of publication are followed by stated date and, in parentheses, actual date if it differs or is more precise. The summaries of content are, of necessity, somewhat uneven; as might be expected, those of notes or brief papers may include details that would not have been mentioned had the work been of greater length. All new names proposed by dos Passos have been included. When new species, subspecies, or forms were named, I have provided the type locality, either the name of the collector of the holotype or the collection from which it was selected (the latter if the collector is not specifically named in the paper), and the holotype repository, all as indicated by dos Passos. All fixations of type localities and designations of lectotypes and neotypes have been documented. In the summaries, names are given the standing accorded to them by dos Passos, and are printed as they appeared in print (forms are italicized, for example).

I am grateful for the extensive assistance of Maria Amália dos Passos and F. Martin Brown, and for the kind cooperation of L. Paul Grey, who has informed me that he holds, entrusted to him by the author, an incomplete dos Passos manuscript not yet prepared for publication.

The following are some abbreviations used: AMNH: American Museum of Natural History, New York City; CM: Carnegie Museum of Natural History, Pittsburgh; USNM: U.S. National Museum, Smithsonian Institution, Washington, D.C.; j.a.: junior author; s.a.: senior author; t.l.: type locality. Postal abbreviations are used for States.

## 1934

1. With L. P. Grey, j.a. A list of the butterflies of Maine with notes concerning some of them. Can. Entomol. 66:188-192, Aug. 1934 (2 Sep. 1934). 110 taxa reported including subspecies, forms.
2. With L. P. Grey, j.a. Additions and corrections to "A list of the butterflies of Maine." Can. Entomol. 66:278, Dec. 1934 (31 Dec. 1934). 7 taxa added; 2 deleted.

## 1935

3. Some butterflies of southern Newfoundland with descriptions of new subspecies (Lepid. Rhopal.). Can. Entomol. 67:82-88, Apr. 1935 (4 May 1935). Discussion of collection made in 1934 by H. McIsaac; *Coenonympha inornata mcisaaci*, n. ssp. (t.l. Doyles Station, Newfoundland, H. McIsaac); *Oeneis jutta terrae-novae*, n. ssp. (t.l. Doyles Station, Newfoundland, H. McIsaac); *Argynnis atlantis canadensis*, n. ssp. (t.l. Doyles Station, Newfoundland, H. McIsaac); *Phyciodes tharos arctica*, n. ssp. (t.l. Table Mountain, Port au Port, Newfoundland, G. C. Hall); all holotypes in AMNH; McIsaac's collection included 21 taxa; 12 additional taxa listed as occurring in Newfoundland.

## 1936

4. Further notes on the butterflies of southern Newfoundland. Can. Entomol. 68:98, May 1936 (6 Jun. 1936). In 1936 H. McIsaac collected 2 species not previously reported from Newfoundland.
5. The life history of *Calephelis borealis* (Lepidoptera). Can. Entomol. 68:167-170, 1 pl. incl. 6 figs., Aug. 1936 (29 Aug. 1936). *C. borealis* appears to be single-brooded in NJ; females observed ovipositing on *Senecio obovatus* Muhlenberg; insect reared; egg, instars of larva, pupa discussed, figured.
6. Some early stages of *Brenthis montinus* Scudder (Lepidoptera—Nymphalidae). Can. Entomol. 68:239-241, 1 pl. incl. 4 figs., Nov. 1936 (5 Dec. 1936). Specimens confined over various plants; all eggs on *Solidago cutleri* Fernald except some on sides of breeding cages; perhaps eggs are dropped on ground, fall into detritus in which larvae, upon emerging, hibernate; egg, first instar larva discussed, figured.

## 1938

7. Some new subspecies of North American Lycaenidae (Lepid.). Can. Entomol. 70:45-48, 1 pl. incl. 16 figs., Mar. 1938 (2 Apr. 1938). Material from various collections described as *Lycaena nivalis browni*, n. ssp. (t.l. Snowslide Canyon, 8 mi [13 km] from Montpelier, ID, W. J. Gertsch); *Plebeius saepiolus gertschi*, n. ssp. (t.l. Cedar Breaks, nr. Cedar City, UT, W. J. Gertsch); *Plebeius icarioides buchholzi*, n. ssp. (t.l. White Mts., AZ, 8500 ft [2591 m], E. Y. Dawson); *Plebeius acmon lutzi*, n. ssp. (t.l. Snowslide Canyon, 8 mi [13 km] from Montpelier, ID, W. J. Gertsch); all holotypes in AMNH; holotypes, allotypes figured.
8. Synonymic notes on *Aglais milberti* (Godart) with the description of a new subspecies (Lepidoptera—Nymphalidae). Can. Entomol. 70:72-73, 1 pl. incl. 6 figs., Apr. 1938 (14 May 1938). Type locality of *A. milberti* fixed; Godart's type figured; *A. m. rothkei* Gunder jr. synonym of *milberti*; *Vanessa furcillata* Say distinct form of *milberti*; *V. m.* var. *subpallida* Cockerell distinct form of *milberti*; Cockerell's type figured; *Aglais m. viola*, n. ssp. (t.l. Doyles Station, Newfoundland, H. McIsaac); holotype in AMNH; holotype, allotype figured.
9. The types of Lepidoptera described by J. D. Gunder. Am. Mus. Novit. No. 999, 16 pp., 26 Jul. 1938. Gunder's collection of North American Lepidoptera (chiefly western Rhopalocera), recently acquired by AMNH, contains type material for 171 of 212 taxa described by him; all types listed; references given to original descriptions, type localities, collectors' names, disposition of types when not at AMNH.
10. A new race of *Euphydryas chalcedona* Dbldy. & Hew. from Arizona (Rhopalocera—Nymphalidae). Can. Entomol. 70:199-200, 1 pl. incl. 4 figs., Oct. 1938 (5 Nov. 1938). Material received for several years as *E. hermosa* (Wright) described as *Euphydryas*

*chalcadona klotsi*, n. ssp. (t.l. Roosevelt Lake, AZ, D. K. Duncan); holotype in AMNH; holotype, allotype figured.

11. A new race of *Basilarchia archippus* Cramer from Louisiana (Rhopalocera—Nymphalidae). Can. Entomol. 70:243, 1 pl. incl. 4 figs., Dec. 1938 (31 Dec. 1938). A previously undescribed "race" in Gulf States, *Basilarchia archippus watsoni*, n. ssp. (t.l. Alexandria, LA, J. Woodgate); holotype in AMNH; holotype, allotype figured.

## 1939

12. A catalogue of the original descriptions of the Rhopalocera found north of the Mexican border. Part two: the Satyridae. Bull. Cheyenne Mountain Mus. 1, part 2, 13 pp., 20 Apr. 1939. Synonymic catalogue with type localities and full citations to descriptions.

## 1940

13. A new subspecies of *Erora laeta* Edwards from Arizona and New Mexico (Rhopalocera: Lycaenidae). Am. Mus. Novit. No. 1052, 2 pp., 15 Mar. 1940. *Erora laeta sanfordi*, n. ssp. (t.l. White Mts., AZ, 8000 ft [2438 m], D. K. Duncan); holotype in AMNH.
14. A new subspecies of *Erebia discoidalis* Kirby (Rhopalocera: Satyridae). Am. Mus. Novit. No. 1053, 2 pp., 22 Mar. 1940. Material from Alberta to AK described as *Erebia discoidalis mcdunnoughi*, n. ssp. (t.l. White Horse, AK, J. A. Kusche); holotype in AMNH.
15. A new species of *Incisalia* from southern California (Rhopalocera, Lycaenidae). Can. Entomol. 72:167–168, Aug. 1940 (31 Aug. 1940). *Incisalia doudoroffi*, n. sp. (t.l. Big Sur, Monterey Co., CA, M. Doudoroff); holotype in AMNH.
16. On the occurrence of *Papilio polydamas* Linnaeus within the United States. Can. Entomol. 72:188, Sep. 1940 (30 Sep. 1940). *P. p. lucayus* not only subspecies in U.S. as *P. p. polydamas* also occurs here; TX specimens in collections acquired by dos Passos.

## 1942

17. With C. D. Michener, s.a. Taxonomic observations on some North American *Strymon* with descriptions of new subspecies (Lepidoptera: Lycaenidae). Am. Mus. Novit. No. 1210, 7 pp., 5 figs., 13 Nov. 1942. *Strymon* of *calanus* group discussed; *S. liparops* (Boisduval & LeConte) synonym of *S. favonius* (J. E. Smith), so species usually called *liparops* becomes *strigosus* Harris; *Strymon strigosus aliparops*, n. ssp. (t.l. Glenwood Springs, CO, Oslar); holotype in AMNH; *S. liparops* (Fletcher) homonym of *liparops* (Boisduval & LeConte), renamed *Strymon strigosus fletcheri*, n. name; lectotype designated (cotype of *Thecla strigosa liparops* Fletcher, USNM); neotype designated for *S. edwardsii* (Grote & Robinson); genitalia figured.
18. With L. P. Grey, j.a. Two new North American subspecies of *Argynnis*, with some revisional notes (Lepidoptera: Nymphalidae). Am. Mus. Novit. No. 1214, 6 pp., 1 fig., 8 Dec. 1942. Material from Gunder collection and others described as *Argynnis utahensis linda*, n. ssp. (t.l. Heyburn Peak, Sawtooth-Boise, ID, 9500–10,000 ft [2896–3048 m], C. W. Herr); *Argynnis coronis carolae*, n. ssp. (t.l. Charleston Park, Clark Co., NE, E. Schiffer); both holotypes in AMNH; both holotypes figured; *A. pfoutsii* Gunder a synonym of *A. platina* Skinner; *A. albrighti* Gunder appears to be form of *A. mcdunnoughi* Gunder, a subspecies of *A. utahensis* Skinner; *A. semivirida* McDunnough correctly placed with *A. nevadensis* W. H. Edwards, a species distinct from *A. utahensis*; *A. chitone* W. H. Edwards a subspecies of *A. hesperis* W. H. Edwards; *A. snyderi* Skinner not a subspecies of *A. coronis* Behr; *A. monticola* Behr a synonym of *A. zerene* Boisduval; *A. malcolmi* Comstock a race of *A. zerene*; *A. conchyliatus* Comstock might be subspecies rather than form of *A. zerene*.

## 1943

19. Some new subspecies of *Incisalia* from North America (Lepidoptera, Lycaenidae). Am. Mus. Novit. No. 1230, 5 pp., 1 Jun. 1943. Scudder, not Minot, is author of

*Incisalia*; type localities fixed for *I. augustus* (Kirby), *I. augustus croestoides* Scudder, *I. iroides* (Boisduval), *I. henrici* (Grote & Robinson), lectotypes designated for these taxa; *Incisalia iroides annetteae*, n. ssp. (t.l. New Mexico, ex J. D. Gunder collection); *Incisalia augustus helenae*, n. ssp. (t.l. Doyles Station, Newfoundland, H. McIsaac); *Incisalia henrici margaretae*, n. ssp. (t.l. 8 mi [13 km] E Deland, FL, B. Heineman); all holotypes in AMNH.

20. A new Riordinid record. Can. Entomol. 75:108, Jun. 1943 (23 Jul. 1943). H. A. Freeman furnished 4 specimens of *Apodemia walkeri* Godman & Salvin, Brownsville, TX, 2–9 Jun. 1940, a new U.S. record.
21. A correction. Can. Entomol. 75:178, Sep. 1943 (21 Oct. 1943). In 3 above *Polygonia comma* (Harris) reported from Newfoundland; specimens were *P. marsyas* (W. H. Edwards).

## 1945

22. Some collections of Lepidoptera. J. New York Entomol. Soc. 53:62, Mar. 1945 (4 May 1945). Since 1935 dos Passos acquired collections of E. H. Blackmore, Victoria, British Columbia; T. E. Bean (IL, Alberta material); M. Rothke, Scranton, PA; R. F. Sternitzky, San Francisco, CA; O. Bryant (including his Arctic material); L. Doerfel, Newark, NJ; most paratypes retained; other types now in AMNH.
23. With L. P. Grey, j.a. A new species and some new subspecies of *Speyeria* (Lepidoptera, Nymphalidae). Am. Mus. Novit. No. 1297, 17 pp., 30 figs., 10 May 1945. Material from various collections described as *Speyeria wenona*, n. sp. (t.l. Cerro Potosi, Municipio de Galeana, Nuevo Leon, Mexico, 12,000 ft [3658 m], R. A. Schneider); *Speyeria cybele letona*, n. ssp. (t.l. City Creek Canyon, Salt Lake City, UT, 4500 ft [1372 m], W. L. Phillips); *Speyeria coronis simaetha*, n. ssp. (t.l. Black Canyon, Cascade Mts., nr. Brewster, WA, J. C. Hopfinger); *Speyeria zerene myrtleae*, n. ssp. (t.l. San Mateo, CA, W. F. Breeze); *Speyeria z. sinope*, n. ssp. (t.l. Estes Park area, Rocky Mt. National Park, CO, 8000 ft [2438 m], R. Weist); *Speyeria z. cynna*, n. ssp. (t.l. Humboldt National Forest, Ruby Valley, Elko Co., NV, E. Schiffer); *Speyeria callippe elaine*, n. ssp. (t.l. Butte Falls, OR, ex J. D. Gunder collection); *Speyeria c. sierra*, n. ssp. (t.l. Gold Lake, Sierra Co., CA, C. Hill); *Speyeria c. harmonia*, n. ssp. (t.l. Mt. Wheeler, Snake Range, nr. UT border, NV, 8000 ft [2438 m], ex J. D. Gunder collection); *Speyeria montiviga* [sic.] [*montiviga*] *secreta*, n. ssp. (t.l. Estes Park area, Rocky Mt. National Park, CO, 8000 ft [2438 m], R. Weist); *Speyeria hydaspe conquista*, n. ssp. (t.l. Little Tesuque Canyon, nr. Sante Fe, NM, 8000 ft [2438 m], A. B. Klots); *Speyeria atlantis lurana*, n. ssp. (t.l. Harney Peak, Black Hills, SD, A. C. Frederick); *Speyeria a. wasatchia*, n. ssp. (t.l. Payson Canyon, Payson, UT, L. D. Pfouts); *Speyeria a. tetonia*, n. ssp. (t.l. Teton Mts., WY, ex J. D. Gunder collection); *Speyeria a. viola*, n. ssp. (t.l. Trail Creek, Sawtooth Mts., ID, 7400 ft [2256 m], C. W. Herr); all holotypes in AMNH; all holotypes figured.
24. With L. P. Grey, j.a. A genitalic survey of Argynninae (Lepidoptera, Nymphalidae). Am. Mus. Novit. No. 1296, 29 pp., 54 figs., 14 Sep. 1945. Genitalia generally discussed, distinctive characteristics given for genera *Boloria* (21 species), *Brenthis* (3 species), *Argynnis* (18 species), *Speyeria* (7 species), *Euptoieta* (2 species); 3 independent genitalic studies of Argynninae conducted (present and those of B. C. S. Warren and F. A. T. Reuss); agreements and disagreements reviewed; *Brenthis* and *Argynnis* should be restricted to Palearctic species; Palearctic *Brenthis* should be set apart from Holarctic *Boloria*, which may require several genera or subgenera; Nearctic *Speyeria* distinct from *Argynnis*; genitalia figured.

## 1946

25. "1945." The photography of types of Lepidoptera. Bull. Brooklyn Entomol. Soc. n.s. 40:166–169, 4 figs., Dec. 1945 (15 Mar. 1946). Improvement on apparatus of J. D. Gunder described, illustrated; type specimens may be photographed with all their labels, without reflections, shadows; cooperative effort proposed to photograph all types of Lepidoptera.
26. With B. C. S. Warren, s.a., and L. P. Grey. Supplementary notes on the classification



of Argynnisinae (Lepidoptera, Nymphalidae). Proc. Roy. Entomol. Soc. London ser. B, 15:71-73, 15 Jun. 1946. New tribal division, Boloriidi, proposed to include *Boloria*, *Proclossiana*, *Clossiana*; the other tribe, Argynnidi, includes *Brenthis*, *Yramea*, *Issoria*, *Speyeria*, *Fabriciana*, *Mesoacidalia*, *Damora*, *Pandoriana*, *Childrena*, *Argyreus*, *Argyronome*; Reuss's *Neoacidalia* synonym of *Speyeria*.

## 1947

27. Notes on Grinnell's types of *Erynnis* Schrank (Lepidoptera, Hesperiiidae). Am. Mus. Novit. No. 1337, 3 pp., 24 Feb. 1947. *E. callidus* (Grinnell) should include *E. c. callidus* (Grinnell), *E. c. pernigra* (Grinnell), *E. c. lilius* (Dyar); lectotype designated for *Thanaos callidus* Grinnell.
28. *Erebia youngi* Holland, its subspecies and distribution (Lepidoptera, Satyridae). Am. Mus. Novit. No. 1348, 4 pp., 14 Jul. 1947. *E. herscheli* Leussler a subspecies of *E. youngi* Holland; *Erebia y. rileyi*, n. ssp. (t.l. Mt. McKinley National Park, AK, ex J. D. Gunder collection); holotype in AMNH.
29. With L. P. Grey, j.a. Systematic catalogue of *Speyeria* (Lepidoptera, Nymphalidae) with designations of types and fixations of type localities. Am. Mus. Novit. No. 1370, 30 pp., 12 Dec. 1947. 109 names published prior to end of 1946 found attributable to *Speyeria*; these represent 13 valid species; remaining 96 names considered subspecies; 58 synonyms; valid species are *S. diana* (Cramer), *S. cybele* (Fabricius), *S. aphrodite* (Fabricius), *S. idalia* (Drury), *S. nokomis* (W. H. Edwards), *S. edwardsii* (Reakirt), *S. coronis* (Behr), *S. zerene* (Boisduval), *S. callippe* (Boisduval), *S. egleis* (Behr), *S. atlantis* (W. H. Edwards), *S. hydaspe* (Boisduval), *S. mormonia* (Boisduval); checklist followed by catalogue, in which names and citations supplemented by type localities, deposition of types, distribution, references to figures, descriptions of preparatory stages when applicable; *Speyeria mormonia eurynome* ab. *igeli*, n. name (type is type of *Argynnis eurynome* ab. *eris* Igel); *Speyeria mormonia eurynome* ab. *fieldi*, n. name (type is type of *Argynnis eurynome clio* trans. form *gunderi* Field); type localities fixed for *S. diana* (Cramer), *S. c. cybele* (Fabricius), *S. a. aphrodite* (Fabricius), *S. a. alcestis* (W. H. Edwards), *S. idalia* (Drury), *S. n. nokomis* (W. H. Edwards), *S. edwardsii* (Reakirt), *S. c. coronis* (Behr), *S. c. snyderi* (Skinner), *S. c. halycone* (W. H. Edwards), *S. z. zerene* (Boisduval), *S. z. hippolyta* (W. H. Edwards), *S. z. platina* (Skinner), *S. c. callippe* (Boisduval), *S. c. rupestris* (Behr), *S. c. juba* (Boisduval), *S. c. laurina* (Wright), *S. e. egleis* (Behr), *S. e. adiate* (W. H. Edwards), *S. a. atlantis* (W. H. Edwards), *S. a. hesperis* (W. H. Edwards), *S. a. irene* (Boisduval), *S. a. electa* (W. H. Edwards), *S. a. lais* (W. H. Edwards), *S. h. hydaspe* (Boisduval), *S. h. rhodope* (W. H. Edwards), *S. m. mormonia* (Boisduval), *S. m. erinna* (W. H. Edwards), *S. m. arge* (Strecker), *S. m. artonis* (W. H. Edwards), *S. m. eurynome* (W. H. Edwards), and in synonymies for *Papilio daphnis* Cramer, *P. daphnis* Martyn, *Argynnis cypris* W. H. Edwards, *A. monticola* Behr, *A. liliana* var. *baroni* W. H. Edwards, *A. wrighti* Wright, *A. nevadensis* r. *meadii* trans. form *gerhardi* Gunder, *A. adiante* Boisduval, *A. montivaga* Behr 1863, *A. montivaga* Behr 1864, *A. astarte* W. H. Edwards 1862, *A. astarte* W. H. Edwards 1864, *A. cornelia* W. H. Edwards, *A. clio* W. H. Edwards, and *A. eurynome* trans. form *brucei* Gunder; types designated in synonymies for *A. astarte* W. H. Edwards 1862, *A. astarte* W. H. Edwards 1864, *A. montivaga* Behr 1864; lectotypes designated for *S. cybele carpenterii* (W. H. Edwards), *S. c. charlottii* (Barnes), *S. aphrodite alcestis* (W. H. Edwards), *S. a. columbia* (Hy. Edwards), *S. nokomis nitocris* (W. H. Edwards), *S. n. coerulescens* (Holland), *S. edwardsii* (Reakirt), *S. c. coronis* (Behr), *S. c. semiramis* (W. H. Edwards), *S. c. snyderi* (Skinner), *S. z. zerene* (Boisduval), *S. z. hippolyta* (W. H. Edwards), *S. z. behrensi* (W. H. Edwards), *S. z. bremnerii* (W. H. Edwards), *S. z. platina* (Skinner), *S. c. callippe* (Boisduval), *S. c. liliana* (Hy. Edwards), *S. c. rupestris* (Behr), *S. c. juba* (Boisduval), *S. c. laura* (W. H. Edwards), *S. c. nevadensis* (W. H. Edwards), *S. c. macaria* (W. H. Edwards), *S. c. meadii* (W. H. Edwards), *S. e. egleis* (Behr), *S. e. adiate* (W. H. Edwards), *S. e. atossa* (W. H. Edwards), *S. e. oweni* (W. H. Edwards), *S. a. atlantis* (W. H. Edwards), *S. a. hesperis* (W. H. Edwards), *S. a. nikias* (Ehrmann), *S. a. nausticaa* (W. H.

Edwards), *S. a. chitone* (W. H. Edwards), *S. a. irene* (Boisduval), *S. a. lais* (W. H. Edwards), *S. h. hydaspe* (Boisduval), *S. h. rhodope* (W. H. Edwards), *S. h. sakuntala* (Skinner), *S. m. mormonia* (Boisduval), *S. m. bischoffii* (W. H. Edwards); *S. m. opis* (W. H. Edwards), *S. m. washingtonia* (Barnes & McDunnough), *S. m. erinna* (W. H. Edwards), *S. m. arge* (Strecker), *S. m. artonis* (W. H. Edwards), *S. m. eurynome* (W. H. Edwards), and *S. m. luski* (Barnes & McDunnough), and in synonymies for *A. cypris* W. H. Edwards, *A. monticola* Behr, *A. inornata* W. H. Edwards, *A. wrighti* Wright, *A. adiante* Boisduval, *A. montivaga* Behr 1863, and *A. atlantis* ab. *chemo* Scudder; neotypes designated for *S. cybele leto* (Behr), *S. a. aphrodite* (Fabricius), *S. idalia* (Drury), *S. n. nokomis* (W. H. Edwards), *S. coronis halcyone* (W. H. Edwards), and in synonymies for *P. daphnis* Cramer, *P. daphnis* Martyn, *A. aphrodite* f. *arizonensis* Elwes, *A. clio* W. H. Edwards.

## 1948

30. The eye colors of some *Colias* collected in New Jersey (Lepidoptera, Pieridae). Proc. Entomol. Soc. Washington 50:35-38, Feb. 1948 (27 Feb. 1948). 53% of individuals of *C. philodice-eurytheme* complex collected near Mendham had black eyes, 47% yellow-green when alive; percentages given by sex; no references found to black eyes in complex; yellow-green is normal color.
31. The care of a collection and library. Lepid. News 2:27, Mar. 1948 (6 Apr. 1948). Hints for protection, maintenance of entomological collections, leather bindings.
32. Critics and criticisms. Lepid. News 2:41, Apr. 1948 (7 Jun. 1948). Ethics of scientific criticism, prompted by short critical reviews included in notices of current entomological literature in *News*.
33. Notes on the disappearance of *Polygonia gracilis* at Rangeley, Maine, in 1947. Lepid. News 2:59, May 1948 (30 Jun. 1948). Very wet spring had serious effect on all 3 *Polygonia* species at Rangeley (*faunus*, *progne*, *gracilis*); no adults seen during summer; *gracilis*, a rare and local insect, may not reappear.
34. The occurrence of anthoxanthins in the wing pigments of some Nearctic *Oeneis* (Rhopalocera: Satyridae). Entomol. News 59:92-96, Apr. 1948 (2 Jul. 1948). Chemistry of pigments in wings of Nearctic *Oeneis* assists greatly in their systematic arrangement without conflicting with result obtained by genitalic examination; presence of anthoxanthins in scales of *O. uhleri* (Reakirt) and *O. taygete* Geyer groups suggests need for rearrangements; *O. nahanni* Dyar a subspecies of *uhleri* or should be placed next to it; *O. chryxus ivallda* (Mead) should have specific standing; describes test for anthoxanthins not injurious to specimens.

## 1949

35. New butterflies from Mount McKinley National Park, Alaska, with a review of *Erebia rossii* (Rhopalocera, Satyridae). Am. Mus. Novit. No. 1389, 17 pp., 28 figs., 6 Jan. 1949. *Oeneis mckinleyensis*, n. sp. (t.l. McKinley Park, AK, ex C. F. dos Passos collection); holotype in AMNH; holotype, allotype, 3 paratypes figured; subspecies of *E. rossii* (Curtis) reviewed, lectotype designated for *E. r. kuskoquima* Holland; *Erebia r. gabrieli*, n. ssp. (t.l. Mount McKinley Park, AK, 3500 ft [1067 m], ex G. P. Engelhardt and C. F. dos Passos collections); holotype in AMNH; holotype, allotype, 2 paratypes figured.
36. The distribution of *Oeneis taygete* Geyer in North America with descriptions of new subspecies (Lepidoptera, Satyridae). Am. Mus. Novit. No. 1399, 21 pp., 16 figs., 26 Jan. 1949. Type locality fixed for *O. taygete*, neotype designated; *Oeneis t. gaspeensis*, n. ssp. (t.l. Mt. Albert, Quebec, A. E. Brower); holotype in AMNH; *Oeneis t. fordii*, n. ssp. (t.l. Kuskokwim River, AK, A. Stecker); holotype in CM; *Oeneis t. edwardsi*, n. ssp. (t.l. San Juan Mts., Hinsdale Co., CO, B. Rotger); holotype in AMNH; holotypes, allotypes figured.
37. [Letter to editor.] Lepid. News 3:19-20, Feb. 1949 (7 Apr. 1949). Actions of Section on Nomenclature and F. Hemming in amending *Règles* at 1948 International Congress of Zoology defended against criticisms of C. W. Sabrosky.

38. The photography of types of Lepidoptera. *Lepid. News* 3:41-42, 1 fig., Apr.-May 1949 (11 Jul. 1949). Revision and condensation of 25 above.
39. A visit to the home of the late William Henry Edwards at Coalburg, West Virginia. *Lepid. News* 3:61-62, 1 fig., Jun. 1949 (23 Sep. 1949). Account of visit to State Dept. of Archives and History, Charleston, WV, to consult Edwards' journals, notebooks, other papers; and to house the entomologist built in 1869, where other Edwards manuscripts examined; figure depicts house.
40. Notes on two *Incisalia* types (Lepidoptera, Lycaenidae). *Can. Entomol.* 81:180-181, Jul. 1949 (25 Oct. 1949). Neotypes designated for *I. hadros* Cook & Watson, *I. henrici* var. *solatus* Cook & Watson.

## 1950

41. A correction. *Lepid. News* 4:15, 1950 (20 May 1950). dos Passos erred in note to literature abstract in *News* 3:109; combination *Malacosoma fragile* correct as to gender.
42. Lepidopterology. Butterflies and Moths: Trans. Lepid. Soc. Japan 1:40-42, Aug. 1950.\* Summary of current American activity in letter invited by journal editor; translated by him into Japanese.
43. With D. B. Stallings, s.a. The Lepidopterists' Society: Report of the Organization Committee. *Lepid. News* 4:38, 1950 (16 Nov. 1950). Committee formed to consider proposed constitution and by-laws drafted by dos Passos completed work, submits finished texts for Society ratification; temporary Society officers appointed.

## 1951

44. The entomological reminiscences of William Henry Edwards with an introduction and annotations. *J. New York Entomol. Soc.* 59:129-186, Sep. 1951 (23 Aug. 1951). Previously unpublished autobiographical MS written by Edwards in old age, edited and with introduction by dos Passos.
45. On the proposal that the trivial name "*ajax*" Linnaeus, 1758 (as published in the binomial combination "*Papilio ajax*") should be suppressed by the International Commission on Zoological Nomenclature under its plenary powers. [Reference Z. N. (S.) 192.] *Bull. Zool. Nomen.* 2:349-350, 28 Sep. 1951. In recent years *ajax* used for 2 different Nearctic butterflies which have valid names, *Papilio polyxenes asterius* Stoll and *P. marcellus* Cramer; *ajax* not properly applicable to either; it is desirable to suppress name.

## 1952

46. Application to the International Commission on Zoological Nomenclature to reconsider and rephrase in part their decision suspending the "Règles" concerning "*Papilio plexippus*" Linnaeus, 1758, insofar as that decision refers to a figure in Holland's "Butterfly book." [Reference Z. N. (S.) 323.] *Bull. Zool. Nomen.* 6:278-283, 23 Jul. 1952. Original description of *P. plexippus* applies to 2 species, 1 American, 1 Oriental; Commission decided to apply name to the American species, as figured by W. J. Holland in *Butterfly book*; Holland's figure of *Danaus plexippus menippe* (Hübner), so when Opinion is rendered reference should be made to an accurate figure of *D. p. plexippus* (Linnaeus).
47. With L. P. Grey, s.a., and A. B. Klots. The "*niobe*/*cydippe*/*adippe*" problem (Class Insecta, Order Lepidoptera, Family Nymphalidae) with suggestions for its solution. [Reference Z. N. (S.) 79.] *Bull. Zool. Nomen.* 6:323-325, 29 Aug. 1952. *Papilio niobe* Linnaeus 1758 presents no nomenclatorial problem; *P. cydippe* Linnaeus 1761, a synonym of *niobe*, long misdetermined as a different butterfly, the "High Brown Fritillary"; *P. adippe* Linnaeus 1767, a new name for *cydippe* and synonym of *niobe*, also misdetermined as "High Brown Fritillary"; to settle scientific name of latter, Commission should suppress certain usages, validate name *adippe* for insect as from 1775 when used by Denis & Schiffermüller.
48. [Book review.] *Die Schmetterlinge Mitteleuropas*. By Walter Forster & Theodor

A. Wohlfahrt. *Lepid. News* 6:79–80, 1952 (17 Nov. 1952). First installments of vols. 1 and 2 reviewed.

49. In support of the application to suspend the rules to (a) validate seven generic names of Linnaeus as of 1758, and designate their type species (b) suppress the generic name "*Phalaena*" Linnaeus, 1758, give preference to its typical subgenus "*Noctua*," declare "*Noctuidae*" the correct name for the family, and (c) validate one generic name of Linnaeus as of 1767 and designate its type species (Class Insecta, Order Lepidoptera). [Reference Z. N. (S.) 462.] *Bull. Zool. Nomen.* 9:153–154, 30 Dec. 1952. Generic names in question except *Phalaena* (*Bombyx*, *Noctua*, *Geometra*, *Pyrallis*, *Tortrix*, *Tinea*, *Alucita*) in constant use for very long time; to upset their usage would cause greater confusion than uniformity; unfortunate to suppress *Phalaena* but not to do so will result in suppressing almost equally well-known *Noctua*; advisable to settle *Bombyx* and *Pyrallis* as generic names as of 1758.

## 1953

50. [Book review.] *Die Schmetterlinge Mitteleuropas*. By Walter Forster & Theodor A. Wohlfahrt. *Lepid. News* 7:26, 1953 (20 Apr. 1953). Second installments of vols. 1 and 2 reviewed.
51. Shall the "Règles" be amended so as to regulate the fixation of type localities and if so upon what terms and conditions? [Document 1/58.] *Bull. Zool. Nomen.* 8:102–108, 25 Jun. 1953. F. Hemming suggested that to reduce instability provisions should be added concerning fixation of type localities; fixation of localities a well-established, desirable practice; rules proposed; some Hemming ideas questioned as basis for discussion of article to amend *Règles*.
52. On the question whether and subject to what conditions the concept of a "neotype" should be officially recognized by an appropriate amendment to the "Règles." [Document 2/13.] *Bull. Zool. Nomen.* 8:121–127, 30 Jun. 1953. In recent years it has been practice among some zoologists to designate neotypes when types lost or destroyed; arguments presented for recognition of neotypes; rules proposed, comments made on F. Hemming's suggestions regarding neotypes as basis for discussion of article to amend *Règles*.

## 1954

53. With F. Hemming, s.a. Proposed limitation to the purposes of the law of priority of the suppression of the name "*Argus*" Bohadsch, 1761 (Class Gastropoda) effected in "Opinion" 185, in order to prevent the confusion which would otherwise arise in the Class Insecta, Order Lepidoptera. [Reference Z. N. (S.) 714.] *Bull. Zool. Nomen.* 9:281–283, 22 Oct. 1954. An Opinion of Commission suppressed for all nomenclatorial purposes generic name *Argus* Bohadsch 1761, and unless action taken, *Argus* Scopoli 1763 becomes available for a genus of Lepidoptera, replacing either *Lysandra* Hemming 1933 or *Polyommatus* Latreille 1804; either result would cause serious confusion; proposals submitted to restrict previous decision to prevent emergence of *Argus* Scopoli.
54. With E. L. Bell, s.a. The lectotype of *Megathymus aryxna* Dyar (Lepidoptera, Megathymidae). *Am. Mus. Novit.* No. 1700, 5 pp., 20 Dec. 1954. Opinions differ as to what constitutes type series of *M. aryxna* and which specimen is lectotype because Dyar did not designate holotype in description; history reviewed and it is concluded lectotype is specimen figured by H. Druce in Lepidoptera-Heterocera section of *Biologia Centrali-Americana*, ed. F. D. Godman & O. Salvin; this permits recognition of *M. evansi* Freeman as valid name.

## 1955

55. "1954." [Book review.] *Die Schmetterlinge Mitteleuropas*. By Walter Forster & Theodor A. Wohlfahrt. *Lepid. News* 8:170–171, 1954 (7 Jan. 1955). Third, fourth, fifth installments of vols. 1 and 2 reviewed.
56. With E. L. Bell, j.a. Request for a ruling as to the specimen to be accepted as the lectotype of "*Megathymus aryxna*" Dyar, 1905 (Class Insecta, Order Lepidoptera).



[Reference Z. N. (S.) 889.] Bull. Zool. Nomen. 11:289–294, 30 Dec. 1955. Bell and dos Passos (54 above) identified lectotype as specimen figured by H. Druce; in same year D. B. Stallings and J. R. Turner identified lectotype as specimen in USNM to which Dyar attached label stating the name *aryxna* was restricted to that specimen; arguments presented against latter conclusion and for former; suggested ruling provided to Commission.

## 1956

57. A bibliography of general catalogues and check lists of Nearctic Rhopalocera. Lepid. News 10:29–34, 1956 (10 Aug. 1956). "Catalogue" and "check list" defined and discussed in introduction followed by chronologically arranged bibliography of 78 items including "not only the strictly Nearctic works but also all general Palaearctic check lists and catalogues that refer to . . . circumpolar insects."

## 1957

58. "1955." With L. P. Grey, j.a. A new name for *Argynnis lais* Edwards (Lepidoptera, Rhopalocera). J. New York Entomol. Soc. 63:95–96, 1955 (8 Mar. 1957). *A. lais* W. H. Edwards 1883 a primary homonym of *A. lais* Scudder 1875; insect renamed *Speyeria atlantis helena*, n. name (type is lectotype of *A. lais* W. H. Edwards in CM); question arises whether new name for a homonym should be proposed in original genus in which homonym described or in genus to which homonym transferred, and it would be well to amend *Règles* to cover the problem.
59. A newly discovered announcement of the proposed publication of the *Sammlung exotischer Schmetterlinge* by Jacob Hübner. J. Soc. Bibliog. Nat. Hist. 3:206, 2 pls., Jan. 1957\* (date stamps suggest U.S. receipt mid-May 1957). dos Passos' incomplete copy of Hübner's Ziefer volume of text (1805–[1823]) to the *Sammlung europäischer Schmetterlinge* (1796–[1838]) contained 2-page letter press announcement dated 21 Sep. 1806 of proposed publication of the work on exotics; announcement donated to AMNH; plates reproduce the pages.
60. "1956." Additions and corrections to "A bibliography of general catalogues and check lists of Nearctic Rhopalocera." Lepid. News 10:213–214, 1956 (21 Jun. 1957). 14 entries added, typos corrected.
61. "1956." William Phillips Comstock, 1880–1956. J. New York Entomol. Soc. 64:1–5, 1 pl. (portrait), 1956 (23 Dec. 1957). Obituary, bibliography.

## 1958

62. With A. B. Klots, j.a. Proposal for the amendment of Article 28 of the existing "Règles" as amended at Copenhagen (1953) so as to give preference to the principle of page priority in the selection of generic and specific names and for other purposes. [Reference Z. N. (S.) 1291; Document 15/1.] Bull. Zool. Nomen. 15:285–292, 11 Feb. 1958. Argument in favor of reinstating "page precedence principle" in place of "first reviser principle"; page and line priority objective, while first reviser principle highly subjective; when 2 or more names proposed at same time in same publication for same genus or other taxon, first name published should prevail; text proposed for draft *Règles* which provides page, line, word precedence.
63. In W. I. Follett. Views of the committees on nomenclature: (a) of the American Society of Ichthyologists and Herpetologists; and (b) of the Society of Systematic Zoology on the relative status of specific names based on modern patronymics having the terminations "-i" and "-ii" respectively. [Document 32/4.] Bull. Zool. Nomen. 15:677–685, 18 Apr. 1958. Follett publishes statements by 12 taxonomists; dos Passos' opinion (p. 681) is that original spellings whether ending in -i or -ii should be retained without emendation; -i ending should be recommended to authors but if they do not use it their spellings should be valid and not subject to emendation; second similar name in a genus whether ending in -ii or -i or vice versa should be considered junior homonym.
64. With A. B. Klots, j.a. Proposal for the amendment of Article 21 of the "Règles" (i.e. Draft Article 22) so as to make its operation entirely objective in cases where a



person other than the nominal author of the book or paper concerned is responsible for a name and its indication, definition or description. [Reference Z. N. (S.) 1326; Document 34/1.] Bull. Zool. Nomen. 15:695–702, 25 Apr. 1958. Article should state that author of scientific name is person who publishes it in connection with indication, definition, description, unless express statement in same publication that some other person responsible; if 1 person responsible for name and another for rest, that shall constitute joint authorship; text proposed.

65. "1957." [Book review.] *Die Schmetterlinge Mitteleuropas*. By Walter Forster & Theodor A. Wohlfahrt. Lepid. News 11:176, 1957 (13 May 1958). Sixth installment of vol. 2 reviewed.
66. Proposals for the amendment and correction of the draft "Règles" concerning the establishment of neotypes (Article 20). [Document 41/3.] Bull. Zool. Nomen. 15: 816–821, 23 May 1958. Provisions regarding neotypes reviewed, thought too strict, impracticable; language proposed in Bradley draft should be adopted with exception of several provisions, cited but not quoted.
67. Article 22, Section 5(c)(1) and Section 6(b). [Reference Z. N. (S.) 1344; Document 42/1.] Bull. Zool. Nomen. 15:824, 23 May 1958. Regarding draft *Règles*, citation of dates when generic combination changed, dos Passos gives examples of what he considers proper citations; in new combinations author's name only should appear in parentheses, not date.
68. Proposed relaxation of the ban on intemperate language and proposed relaxation of the ban on names calculated to give personal and other types of offence. [Reference Z. N. (S.) 1296; Documents 19/3 and 23/3.] Bull. Zool. Nomen. 15:857, 23 May 1958. Elimination of these provisions may lead some to assume falsely that zoologists have come to feel differently about such matters; matters could be treated as effectively by omitting them from present position in *Règles*, incorporating them in Code of Ethics.
69. Support for the proposal included by Professor Chester Bradley in the suggested annexe to Subsection (6) of Section 4 of Article 7 of the draft "Règles." [Reference Z. N. (S.) 1348; Document 44/1.] Bull. Zool. Nomen. 15:935, 13 Jun. 1958. Regarding status of names in preprints when paper concerned not published later in regular manner, dos Passos agrees with Bradley's addition, suggests it be made to apply after a certain date.
70. Citation of corrected and emended names. [Z. N. (S.) 1269; Document 9/3.] Bull. Zool. Nomen. 15:974, 13 Jun. 1958. Regarding draft *Règles*, when scientific name misspelled or otherwise written incorrectly, all emendations should be noted as such; in appropriate cases incorrect spelling should be placed in synonymy followed by *lapsus calami*.
71. Citation of dates in round brackets for bibliographical references. [Reference Z. N. (S.) 1294; Document 17/4.] Bull. Zool. Nomen. 15:975, 13 Jun. 1958. Regarding draft *Règles*, dos Passos objects to proposed deletion of Article 22, Recommendation 10(B) relating to citation of dates; Paris decisions concise, logical, not restrictive, pedantic; provide instant knowledge where to find a citation.
72. In R. V. Melville. [Draft "Règles," Article 28, Section 4(a): The diaeresis symbol, Reference Z. N. (S.) 1013; Document 72/1.] Bull. Zool. Nomen. 15:1158–1162, 2 Jul. 1958. In draft, diaeresis symbol excluded from category of diacritic marks; Melville publishes statements by 3 taxonomists; dos Passos' opinion (p. 1161) is that diaeresis symbol be retained.
73. The Satyrid butterflies of northwestern North America (Lepidoptera: Satyridae). Proc. Tenth Intern. Congr. Entomol., Montreal, August 17–25, 1956 1:673–681, Dec. 1958. Survey of species of *Coenonympha*, *Cercyonis*, *Oeneis*, *Erebia* of AK, Yukon, British Columbia, western Alberta; brief history of collecting in area followed by discussion of each biotic province, catalogue with references.

1959

74. "1958." Frank Edward Watson, 1877–1947. J. New York Entomol. Soc. 66:1–6, Mar.–Jun. 1958 (20 Jan. 1959). Biographical sketch, bibliography.

75. "1958." The dates and authorships of the names proposed in volume 9 of *Encyclopédie méthodique* by Godart and Latreille, 1819–[1824]. *Lepid. News* 12:119–120, 1958 (26 Jan. 1959). Although title of work dated 1819, only first part published that year; all names in it should be ascribed to Godart; second part published in 1824; some of its names should be ascribed to Godart, others to Latreille; explanatory tables of generic and specific names provided.
76. "1958." The dates and authorships to be ascribed to the generic and specific names proposed by Boisduval and LeConte and by LeConte alone in the *Lépidoptères de l'Amerique septentrionale*, 1829–1833–[1834]. *Lepid. News* 12:121–122, 1958 (26 Jan. 1959). Discovery of a set of the work in original wrappers and other research resulted in new evidence; tables provide authorship, dates of names.
77. "1958." The authorship of the names proposed in the *Natural history of the rarer lepidopterous insects of Georgia* (1797). *Lepid. News* 12:191–192, 1958 (30 Apr. 1959). Internal evidence reveals relative roles of J. E. Smith and J. Abbot in producing work; Smith explains he alone responsible for systematic names, definitions, so all names proposed in book can be attributed to Smith alone.
78. "1958." The authorship and dates of publication of the names of some Rhopalocera proposed in the *Reise der oesterreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorff-Urbair*, 1864–1867–[1875]. *Lepid. News* 12:193–194, 1958 (30 Apr. 1959). Summary of pertinent bibliographical data followed by tables of generic, specific names, dated and ascribed jointly to C. Felder and son R. Felder.
79. "1958." The dates and authorships of some names proposed by Cramer and Stoll in *De uitlandsche kapellen voorkomende in de drie waereld-deelen Asia, Africa en America*, and by Stoll alone in *Aanhangsel van het werk, De uitlandsche kapellen voorkomende in de drie waereld-deelen Asia, Africa en America, door den heere Pieter Cramer* [1775]–1791. *Lepid. News* 12:195–198, 1958 (30 Apr. 1959). Names cannot be dated from text because many not binomials; specific name often appears alone; names must be dated from indexes (often published later than text) in which generic names appear in conjunction with specific names and references to text figures; table provides pertinent data.

## 1960

80. "1959." Further notes on the dates of publication of some generic and specific names proposed by Boisduval and LeConte in the *Lépidoptères de l'Amerique septentrionale*, 1829–1833–[1834]. *J. Lepid. Soc.* 13:212, 1959 (1 Aug. 1960). Information from correspondent about another copy in wrappers (76 above) led to redating a number of names.
81. Taxonomic notes on some Nearctic Rhopalocera. 1. Hesperioidea. *J. Lepid. Soc.* 14: 24–36, 1960 (15 Dec. 1960). Systematic changes incorporated in forthcoming checklist of Nearctic Rhopalocera explained; contrary to present practice, list will proceed from lower butterflies to higher; result in Hesperioidea is complete reversal of order used by W. H. Evans (1951–55); genera in his work used but there will be changes in systematic arrangement of species; treatment of Papilionoidea will accord more or less with plan of B. C. S. Warren (1947) from lowest to highest; within genera listing of species by J. H. McDunnough (1938) followed except when improvement desirable; most names in recent literature resulting from splitting of genera given subgeneric standing; effort will be made to comply with *Règles* but nomenclature code of N. Banks and A. N. Caudell (1912) preferable to *Règles* in present state, will be followed except when modified by *Règles*; taxonomic notes follow on species within Hesperioidea, in which no new names proposed but some changed in rank or relegated to synonymy, many other corrections made.

## 1961

82. "1960." [Book review.] *Butterflies of Formosa in colour*. By Takashi Shirôzu. *J. Lepid. Soc.* 14:243, 1960 (& Sep. 1961).

## 1962

83. The dates of publication of the *Histoire générale et iconographie des lépidoptères et des chenilles de l'Amerique septentrionale*, by Boisduval and LeConte 1829–1833[–1834]. J. Soc. Bibliog. Nat. Hist. 4:48–56, Jan. 1962\* (date stamps suggest U.S. receipt mid-Feb. 1962). Detailed bibliographical summary of work, including information from 3 copies in original wrappers; review of previous relevant bibliographical contributions followed by tables that apply publication dates of livraisons to scientific names.
84. "1961." Taxonomic notes on some Nearctic Rhopalocera. 2. Papilionoidea. J. Lepid. Soc. 15:209–225, 1961 (19 Jun. 1962). Continuation of 81 above; no new names proposed but some changed in rank or relegated to synonymy, many other corrections made; brief supplemental note to part 1 (Hesperioidea) on p. 225.
85. The authorship of three scientific names of Nearctic Rhopalocera variously credited to Boisduval or Lucas. J. Lepid. Soc. 16:45–46, 1962 (30 Aug. 1962). Authorship of *Papilio eurymedon*, *P. rutulus*, *P. zelicaon* ascribed to P. H. Lucas, who published names before J. Boisduval.

## 1963

86. The status of infrasubspecific names. [Reference Z. N. (S.) 1569.] Bull. Zool. Nomen. 20:67–70, 18 Mar. 1963. New article should be added to *Code* to deal with these names; text proposed, practically same as that in Bradley Draft but not adopted in 1958; if proposal adopted, emendations to Articles 1, 15, 17(9), 45c will be necessary.
87. A name first published as a synonym is not thereby made available. Article 11(d). [Reference Z. N. (S.) 1570.] Bull. Zool. Nomen. 20:70, 18 Mar. 1963. *Code* should be amended to state that a name first published as synonym not thereby made available unless prior to 1958 it has been recognized, removed from synonymy, and used as name of a taxon.
88. Neotypes—Article 75. [Reference Z. N. (S.) 1571; Document 17/1.] Bull. Zool. Nomen. 20:71–72, 18 Mar. 1963. Recognition of neotypes by *Code* was step in right direction but some provisions respecting their designation so strict and unnecessary that article will likely be ignored or workers discouraged from designating neotypes; additions, deletions proposed.
89. Form of citation—Article 51b(1). Date in a changed combination—Article 22, Recommendation 22B. [Reference Z. N. (S.) 1576; Document 22/2.] Bull. Zool. Nomen. 20:77–78, 18 Mar. 1963. Article 51b(1) of *Code* should be amended to state that name of subsequent user of a scientific name, if cited, to be separated by comma; Article 22, Recommendation 22B should be repealed because placing date in parentheses when combination is changed can affect and make improper the date citation which in that particular case should be outside parentheses.
90. *Calephelis* Grote and Robinson, 1869, (Insecta, Lepidoptera): Proposed use of the plenary powers to designate a type-species in conformity with current usage [Reference Z. N. (S.) 1563.] Bull. Zool. Nomen. 20:313–320, 12 Jul. 1963. History of uses of generic names *Nymphidia* Boisduval & LeConte, *Calephelis* Grote & Robinson, *Lephelisca* Barnes & Lindsey for North American riodinids reviewed; it is proposed to retain *Calephelis* with type species *Erycina virginiensis* Guérin-Ménéville and invalidate others.
91. Supplemental notes to previous taxonomic notes on some Nearctic Rhopalocera. J. Lepid. Soc. 17:103–104, 1963 (8 Nov. 1963). Since publication of 2 papers (81 and 84 above) designed to explain systematic changes incorporated in forthcoming checklist of Nearctic Rhopalocera, communications received from other workers; these, other supplemental matters discussed.

## 1964

92. *A synonymic list of the Nearctic Rhopalocera*. N. p. [New Haven, CT], 1964. vi, 145 pp. Lep. Soc. Mem. No. 1 (Feb. 1964, *in litt.*). List "almost a catalogue"; effort made to give generic synonymies in addition to specific, and to cite type species of each generic name used; subjective, objective generic synonyms differentiated; taxa

provided with authors' names, publication dates; 687 species numbered; 1002 subspecies recognized, 1 questioned; 96 species asterisked as "of doubtful North American occurrence"; of these, 89 are species in which nominate subspecies not Nearctic but Nearctic subspecies exist; infrasubspecific names included.

## 1965

93. Peale's *Lepidoptera Americana* (1833). J. New York Entomol. Soc. 73:18-26, 5 figs., Mar. 1965 (19 Apr. 1965). T. R. Peale's work, "the first book begun by an American author on American lepidoptera that was published in this country," discontinued after one number; that part discussed and bibliographically described; 8 copies located; wrappers, subscribers' list illustrated.
94. With H. Ruckes, s.a. In memoriam: Ernest Layton Bell, 1876-1964. J. New York Entomol. Soc. 73:49-56, 1 fig. (portrait), Jun. 1965 (16 Jun. 1965). Obituary, bibliography.
95. Review of the Nearctic species of *Pieris* "*napi*" as classified by androconial scales and description of a new seasonal form (Lepidoptera: Pieridae). J. New York Entomol. Soc. 73:135-137, Sep. 1965 (17 Sep. 1965). As result of B. C. S. Warren's papers on androconial scales and their bearing on speciation in *Pieris*, classification of *P. bryoniae* Ochsenheimer, *P. napi* (Linnaeus), *P. narina* Verity, and subspecies reviewed; *Pieris narina mogollon* gen. aest. *warreni* n. form (t.l. White Mts., AZ, ex F. R. Sternitzky collection); holotype in AMNH.
96. With H. Ruckes, s.a. Ernest Layton Bell (1876-1964). J. Lepid. Soc. 19:190-191, 1965 (24 Sep. 1965). Obituary differing from 94 above.
97. Addenda et corrigenda to the "Synonymic list of Nearctic Rhopalocera." J. Lepid. Soc. 19:192, 1965 (24 Sep. 1965). Page laid into later copies of *Synonymic list* sold by Society.
98. With L. P. Grey, j.a. Notes on certain lectotypes designated by the authors in their Systematic catalogue of *Speyeria* (Lepidoptera: Nymphalidae). Trans. Am. Entomol. Soc. 91:351-360, Sep. 1965 (30 Sep. 1965). Continuation of catalogue, prompted by F. M. Brown's study of argynnid names proposed by W. H. Edwards; lectotypes of *S. coronis coronis* (Behr), *S. callippe inornata* (W. H. Edwards), and *S. atlantis hesperis* (W. H. Edwards) redesignated as neotypes; neotype designated for *S. callippe nevadensis* (W. H. Edwards); lectotype redesignated for *S. mormonia artonis* (W. H. Edwards); neotype redesignated for *S. mormonia clio* (W. H. Edwards).

## 1966

99. The discovery of additional journals of Frank E. Watson. J. New York Entomol. Soc. 74:188, Dec. 1966 (29 Dec. 1966). Entomological journals for 1896-1905, 1914-22, 1926-31, 1934-47 located, donated to AMNH, which now has all Watson journals except those for 1932-33, presumed lost.
100. *Pieris narina oleracera* (Harris) in New Jersey (Lepidoptera: Pieridae). J. New York Entomol. Soc. 74:222-223, Dec. 1966 (29 Dec. 1966). NJ records cited by earlier workers but discounted by later ones as misdeterminations verified by capture of a male by M. A. dos Passos near Springdale, Sussex Co., 8 Jul. 1966.

## 1968

101. With B. C. S. Warren, j.a. The homonymy of *Papilio aglaja* Linnaeus 1758 (Insecta, Lepidoptera, Pieridae and Nymphalidae): Request for validation. Z. N. (S.) 1791. Bull. Zool. Nomen. 25:68-71, 27 Sep. 1968. Linnaeus named 2 insects *P. aglaja* in 1758 ed. of *Systema naturae*, then in 1767 ed. renamed pierid, retained *aglaja* for nymphalid; pierid usage has 1758 page priority over nymphalid usage which is therefore homonym; this long recognized but recent application seeks to resurrect nymphalid name, recognize 2 uses of *aglaja* in different families; situation brought about by adoption of first reviser rule, repeal of priority rule; Linnaeus not reviser in 1767, primary junior homonym not an available name; consequences of decision recognizing 1767 ed. as revision would be chaotic; Commission asked to deny



application insofar as it seeks to suspend rule concerning homonyms and permit 2 uses of name, asked to recognize specific name *charlotta* Haworth for nymphalid, *aglaia* Linnaeus for pierid, and to take other appropriate actions.

## 1969

102. A revised synonymic list of the Nearctic Melitaeinae with taxonomic notes (Nymphalidae). J. Lepid. Soc. 23:115–125, 1969 (29 May 1969). 2 revisions, 1st by H. L. Higgins, 2nd by D. L. Bauer, published before *Synonymic list* (92 above) rendered its arrangement of Melitaeinae genera, species somewhat obsolete, but checklist already in press; revised synonymic list of subfamily presented in format of 92; 8 fewer species-level taxa, owing primarily to relegation to subspecies; taxonomic notes follow to explain changes, placement of names.
103. A name for *Polygonia satyrus marsyas* auctorum (Lepidoptera: Nymphalidae). Trans. Am. Entomol. Soc. 95:153–159, 2 figs., Mar. 1969 (6 Jun. 1969). Misled by false locality labels, W. H. Edwards described European *P. c-album* as American species *marsyas* in 1870; *marsyas* usually considered U.S. West Coast population of *P. satyrus* (W. H. Edwards), so desirable to propose new name for that population, *Polygonia s. neomarsyas*, n. ssp. (t.l. Salmon Meadows, Brewster, WA, J. C. Hopfinger); holotype in dos Passos collection but will be deposited in CM; holotype, allotype figured.
104. With B. C. S. Warren, s.a. The homonymy of *Papilio aglaia* Linnaeus 1758 (Insecta, Lepidoptera, Pieridae and Nymphalidae): Request for validation Z. N. (S.) 1791. A further note in opposition to this application. Bull. Zool. Nomen. 26:67–68, 8 Aug. 1969. Further evidence provided to support application has not established that Linnaeus a first reviser in 1767; not conducive to stability of nomenclature to alter long-accepted usages; application and another to same end should be denied.
105. *Lethe eurydice* (Johansson) and *L. fumosus* (Leussler), sibling species (Lepidoptera: Satyridae). J. New York Entomol. Soc. 77:117–122, Jun. 1969 (24 Oct. 1969). *L. eurydice* has been considered single species with 4 subspecies; rather, 2 sibling species involved which occur in different environments, have constant superficial differences, probably different foodplants; bibliographical synonymies provided for *L. eurydice*, *L. fumosus* n. comb.; species discussed; arrangement of names proposed in checklist form.
106. With A. B. Klots, j.a. The systematics of *Anthocharis midea* Hübner (Lepidoptera: Pieridae). Entomol. Am. 45:1–34, 11 figs., 1969 (29 Dec. 1969). Species placed in subgenus A. (*Falcapica*) Klots; neotypes designated for 3 species-group names available for species: *genutia* Fabricius, *midea* Hübner, *lherminieri* Godart; systematics, geographic variation discussed; bibliographical synonymies provided for species, nominate subspecies; *Anthocharis midea annickae*, n. ssp. (t.l. West Rock, New Haven, CT, C. L. Remington); holotype in AMNH; life history, foodplants, parasites discussed; relevant types figured including holotype, allotype of *annickae*.

## 1970

107. A revised synonymic catalogue with taxonomic notes on some Nearctic Lycaenidae. J. Lepid. Soc. 24:26–38, 1970 (26 Mar. 1970). Revision by H. K. Clench appeared when *Synonymic list* (92 above) in press, rendered its arrangement of Theclinae obsolete; revised synonymic list of subfamily presented in format of 92; *Harkenclenus*, n. g. proposed; taxonomic notes follow to explain changes, placement of names.

## 1972

108. Designation of a lectotype for *Erebia youngi* Holland. Entomol. Rec. J. Var. 84: 238–241, 1 pl. incl. 4 figs., Oct. 1972 (15 Oct. 1972\*). Since Holland's description a very similar Asiatic species, *E. dabanensis* Erschoff, discovered in AK, *E. kozhantshikovi* Sheljuzhko may occur there also; necessary to determine genitally whether these species confused in Holland's type series; on dissection of 2 male syntypes 1 found to be *dabanensis*; 2nd *youngi*, latter designated lectotype; *E. herscheli*



Leussler a local race of *youngi*; *E. youngi rileyi* dos Passos similarly proven to be *dabanensis* so *rileyi* falls as synonym.

## 1973

109. The great advantages of zoological nomenclature as contrasted with the many disadvantages of popular names!?! News. Lepid. Soc. 15 May 1973\*:2-3. In light vein, suggested that many common names more stable than scientific names.
110. The correct name for the subspecies of *Limenitis weidemeyerit* occurring in Arizona (Nymphalidae). J. Res. Lepid. 12:21-24, Mar. 1973 (18 Dec. 1973, *in litt.*) Confusion in literature reviewed; synonymy provided; name *angustifascia* Barnes & McDunnough a jr. synonym of *sinefascia* Dyar et al., the correct name.

## 1974

111. With W. D. Field, s.a., and J. H. Masters. *A bibliography of the catalogs, lists, faunal and other papers on the butterflies of North America north of Mexico arranged by state and province (Lepidoptera: Rhopalocera)*. Washington, DC: Smithsonian Institution Press, 1974. [ii], 104 pp. Smiths. Contrib. Zool. No. 157 (20 Feb. 1974). 2987 selected publications listed in geographical units (Greenland included) and in supplemental bibliography of items that cover more than 1 state or province.
112. With J. R. Heitzman, s.a. *Lethe portlandia* (Fabricius) and *L. anthedon* (Clark), sibling species, with descriptions of new subspecies of the former (Lepidoptera: Satyridae). Trans. Am. Entomol. Soc. 100:52-99, frontis., 20 figs., Mar. 1974 (16 May 1974). *L. portlandia* has been considered as having 4 subspecies and 1 synonym; rather, 2 sibling species involved: *portlandia*, having 3 subspecies (2 named here), *L. anthedon*; the 2 species occur in different environments, have different foodplants; bibliographical synonymies provided for *portlandia*, its nominate subspecies, for *Lethe portlandia floralae*, n. ssp. (t.l. Rock Springs, Orange Co., FL, S. Roman); holotype in AMNH; and *Lethe portlandia missarkae*, n. ssp. (t.l. 5 mi [8 km] S of Fayetteville, Washington Co., AR, 1300 ft [396 m], J. R. Heitzman); holotype in AMNH; the 2 subspecies discussed; most specimens referred to in literature as *portlandia* are *anthedon*, so bibliography provided; arrangement of names proposed in checklist form; holotypes, allotypes of new subspecies figured, as are other relevant types, some genitalia.

## 1977

113. "1976." A note on *Oeneis jutta harperi*, its author and date of publication (Satyridae). J. Res. Lepid. 15:211-213, Dec. 1976\* (date stamps suggest receipt late Apr. 1977). Previous publications of name *harperi* as subspecies of *O. jutta* (Hübner) invalid according to *Code*; name validly published here as *Oeneis j. harperi*, n. ssp.; t.l. fixed; types mentioned in literature presumably in P. W. Chermock collection.
114. A taxonomic note on *Polygonia faunus arcticus* Leussler (Lepidoptera: Nymphalidae). Pan-Pac. Entomol. 53:179-180, Jul. 1977 (28 Nov. 1977). Leussler's *arcticus* is subspecies of *P. hylas*, not *P. faunus*, as type specimens indicate; name should be written as *Polygonia hylas arcticus* Leussler, n. comb.

## 1978

115. Correction—Note on *Polygonia faunus arcticus*. Pan-Pac. Entomol. 54:42, Jan. 1978 (26 Apr. 1978). Phrase concerning type locations added to 114 above.

## 1981

116. A little-known, anonymous work on American and European butterflies and moths (1906), which should be attributed to William Beutenmüller (Lepidoptera: Nymphalidae). J. New York Entomol. Soc. 89:143-145, Jun. 1981 (24 Sep. 1981). Discussion and description of *A manual of American and European butterflies and moths reproduced in natural colors with their common and scientific names*; Mrs. Beutenmüller probably executed plates.

## 1982

117. "1981." With A. B. Klots, s.a. Studies of North American *Erora* (Scudder) (Lepidoptera, Lycaenidae). J. New York Entomol. Soc. 89:295–331, 34 figs., Dec. 1981 (19 Feb. 1982). Genus *Erora* characterized, discussed, as are *E. laeta* (W. H. Edwards), *E. q. quaderna* (Hewitson), *E. q. sanfordi* dos Passos; early stages, ethology, ecology, geographic distribution of *laeta*, *quaderna* *sanfordi* discussed; bibliographical synonymies, lists of distributional records included; early stages, types figured.
118. "1981." Some little-known U.S. publications on Lepidoptera I. [Edited and with abstract and foreword by L. P. Grey.] J. Res. Lepid. 20:111–115, Summer 1981 (20 Sep. 1982). Periodicals *The Lepidopterist* (1916–17), *Lepidoptera* (1918–21), *The Lepidopterist* (1918–31) discussed, known numbers listed with dates of publication, pagination, inclusions.
119. "1981." Some little-known U.S. publications on Lepidoptera II. [Edited and with abstract by L. P. Grey.] J. Res. Lepid. 20:115–122, Summer 1981 (20 Sep. 1982). Information similar to 117 above provided for *The Butterfly Farmer* (1913–14), *Lorquinia* (1916–19), *Southwest Science Bulletin* (1920), *Butterfly Park Nature Club News* (1929–31), *The Lepidopterists' News* (1933), *The Entomologists' Exchange Association* (1936), *The Entomologists' Exchange News* (1937–42), *The Butterfly Club* (1946–47), *Club Notes*, *Moth and Butterfly Club* (?1947–53), *Notes on Moths and Butterflies* (1953–55), for relevant material in *Sierra Club Bulletin* (1913), *Hobbies* (1936).

## 1983

120. With C. D. Ferris, s.a., J. A. Ebner, and J. D. Lafontaine. An annotated list of the butterflies (Lepidoptera) of the Yukon Territory, Canada. Can. Entomol. 115:823–840, 6 figs., Jul. 1983 (22 Jun. 1983, *in litt.*) 95 taxa reported including subspecies; some listed as questionable; various species figured.

BIOLOGY OF *SPEYERIA ZERENE HIPPOLYTA*  
(NYMPHALIDAE) IN A MARINE-MODIFIED  
ENVIRONMENT

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**ABSTRACT.** This paper examines life history and adaptations of *Speyeria zerene hippolyta* (Edwards) along the Oregon and Washington coasts where cold wind, rain, and fog persist during much of the year. The butterfly uses an open grassland habitat on salt-spray meadows and higher headlands adjacent to the ocean, where the larvae feed on the common *Viola adunca* J. E. Smith. Four unusual adaptations to this environment are seen in *S. zerene hippolyta* that are absent from the closely related *S. z. bremnerii* (Edwards) of the inland Willamette Valley: small body size and extensive dark basal suffusion which enhance body heating from solar radiation; normal flight activity under cool, cloudy or foggy conditions; prolonged larval development which coordinates adult emergence with the most favorable weather conditions in late summer and fall; and much individual variation in larval development rate and adult emergence which compensates for variable and unpredictable weather from year to year.

**Additional key words:** *Speyeria zerene bremnerii*, *Viola adunca*, adaptation, grassland, coastal habitat.

*Speyeria zerene* (Boisduval) is a complex polytypic species with 14 recognized subspecies (Grey & Moeck 1962). The subspecies occupy a wide diversity of habitats ranging from coastal rainforests in the Pacific Northwest to arid sagebrush plains in the Great Basin. *Speyeria z. hippolyta* (Edwards), informally known as the "Hippolyta Silverspot" or "Oregon Silverspot", is restricted to a cool, wet, marine-modified environment adjacent to the Pacific Ocean in western Washington and Oregon. This subspecies is of special concern because of its decline toward extinction and its official classification as a threatened species (Hammond & McCorkle 1983).

The closely related *S. z. bremnerii* (Edwards) occupies inland areas of the Pacific Northwest from Vancouver Island S through the Puget Sound trough and Willamette Valley of western Oregon. The primary difference in adult phenotype between these subspecies is the small wing of *S. z. hippolyta* although extinct Oregon populations of *S. z. bremnerii* also differed in having reduced basal suffusion on the dorsal wing surfaces (Fig. 3). In addition, *S. z. hippolyta* differs in several aspects of life history and developmental physiology which appear to be specific adaptations to the coastal environment. An investigation of

these characteristics is the subject of the present paper. It should be noted that both Moeck (1957) and Howe (1975) confused this coastal subspecies with a population of dwarfed *S. z. conchyliatus* (Comstock) endemic to the volcanic ash and pumice fields along the E slope of the Oregon Cascade Range.

## MATERIALS AND METHODS

Field and museum studies were conducted from 1960 to 1986 together with laboratory rearing of larvae. Most public and many private collections in Washington and Oregon were examined. In 1963 and 1964, one of us (McCorkle) developed a technique for rearing *Speyeria* larvae using a modification of a procedure (Magnus 1958) for the European fritillary *Argynnis paphia* L. A variant of the former technique was described by Mattoon et al. (1971), and was used in the present study, except that larvae were kept over winter in hollow wooden blocks and reared in small jars instead of nylon sleeves.

Capture-recapture studies were done at the Rock Creek study site in Lane Co., Oregon, during 1980 using the 1-2-4-7 marking system described by Ehrlich and Davidson (1961). Sex, wing length, general condition, time, place, and type of activity at time of capture and recapture were recorded.

Voucher specimens are deposited in the Systematic Entomology Laboratory at Oregon State University, Corvallis.

## BIOLOGY OF STAGES

### Oviposition

*Speyeria zerene hippolyta* is usually a grassland butterfly that lives on open salt-spray meadows and grassy headlands adjacent to the Pacific Ocean, where the larvae feed on the common blue violet, *Viola adunca* J. E. Smith. Based on more than 100 observations, females oviposit singly among vegetation near host plants. Females are apparently stimulated to oviposit by some volatile compound emanating from violets. We found that females oviposit only in the presence of violets, but that direct physical contact with the host is not necessary. We observed oviposition up to 20 cm downwind of even dried violet leaves.

During oviposition behavior, the butterflies flew near the ground, working their way upwind. When violets were near, they paused to climb in meadow vegetation, probing with curved abdomen until a suitable site was contacted, and an egg deposited. We even observed females crawling into knee-deep layers of grass that overgrew violets by late summer. Oviposition observations and location of larvae indicate that females favor sunny sites, and usually avoid N slopes of steep meadow rises.

Eggs are cream colored when first laid, but if fertile, darken to pinkish tan by the second day. Eggs began to hatch 16 days after oviposition with ambient room temperature varying from 21 to 24°C ( $N = \text{ca. } 1000$ ). A large quantity of lipid is stored in *Speyeria* eggs which appears to serve as a food reserve during larval diapause. This lipid, in the form of a light oil, is readily observed in yolk by dissecting eggs.

### Larva

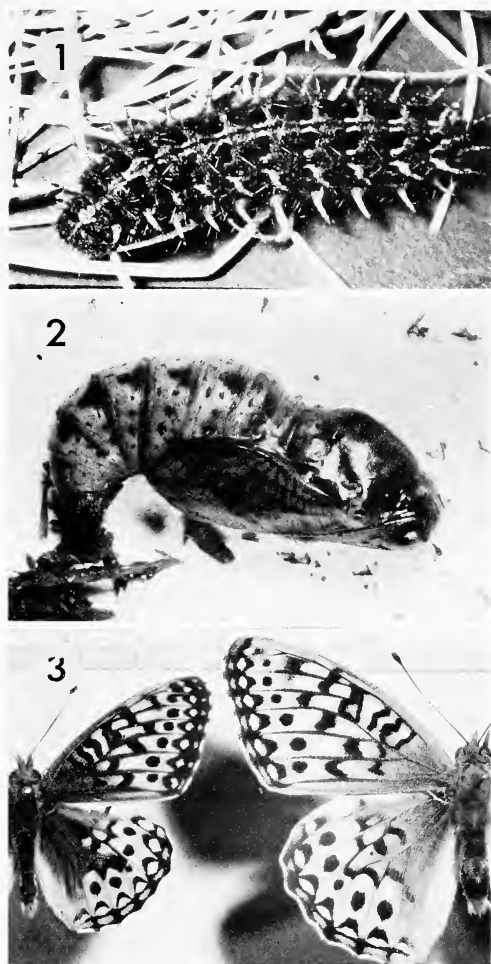
Newly hatched larvae ( $N = \text{ca. } 1000$ ) usually wander short distances. As in other *Speyeria*, first instar *S. z. hippolyta* soon enter a diapause that lasts over winter. After selecting a suitable site, they spin a thin silk mat on which they rest until spring. Larvae exhibit considerable resistance to desiccation during diapause. In the laboratory, they survived a month or more without moisture, but this stress may diminish survival by spring. Thus, in years with delayed fall rains, the earliest hatched larvae may be at a disadvantage. When moisture is available, laboratory larvae touched their mouths to a wet surface, and some nearly doubled in size within a short time.

The following description of the last (6th) instar is based on larvae from about 10 family lines. The spiny larva (Fig. 1) is dark brown with a pair of pale lines running down the back, each of which has a row of black patches running parallel to it on the outside. These black patches are located on both sides of each body segment adjacent to the pale dorsal lines. Lateral parts of the body are finely and irregularly mottled with pale yellow. The head is mostly black, but the occipital area is yellow. Spine bases, especially those of the lateral rows, are straw colored similarly to the lines on the back. This color pattern resembles that of the inland *S. zerene bremnerii* (Hardy 1958), and blends with dried leaves where larvae take refuge when not feeding.

The first instar possesses unbranched setae or hairs. Later instars bear branched spines in the pattern illustrated by Scott and Mattoon (1982) for *S. nokomis* (Edwards). We reared all 13 species of *Speyeria*, and this setal pattern is consistent throughout the genus. However, it should be noted that a lateral spine is present on the 10th abdominal segment that was omitted from the Scott-Mattoon setal map. Superficially, this spine appears to be on the 9th segment. Spine branches or spinules are attached to the primary shaft in such a way that they can swing in toward the shaft apex when the larva withdraws from an entanglement. When pushed outward, the spinules lock into the outstretched position. In larger larvae, these sharp spines may provide protection from predators such as mice and, perhaps, shrews (unpubl. obs.).

In addition to spines, *Speyeria* larvae possess what may also serve as a defense against predators in the form of a fleshy, eversible osmeterium.





FIGS. 1-3. *S. zerene*. 1, Mature 6th instar of *S. z. hippolyta*; 2, Pupa of *S. z. hippolyta*; 3, Reared males of *S. z. hippolyta* (left) and Willamette Valley *S. z. bremnerii* (right).

Whenever this structure is extruded, a disagreeable musky smell becomes apparent. This odor is faint in the small *S. zerene hippolyta*, but is much stronger in larger-bodied species such as *S. coronis* (Behr) and *S. edwardsii* (Reakirt). Unlike the long dorsal osmeteria of papilionid larvae, *Speyeria* osmeteria are short, wedge-shaped organs located ventrally just behind the head and before the first pair of thoracic legs. In addition, the musky smell of *Speyeria* osmeteria is distinctly different from the more pungent, aromatic smell of papilionid osmeteria.

As with most *Speyeria*, older larvae of *S. z. hippolyta* retreat to shelter sites sometimes several centimeters from host violets. These sites may

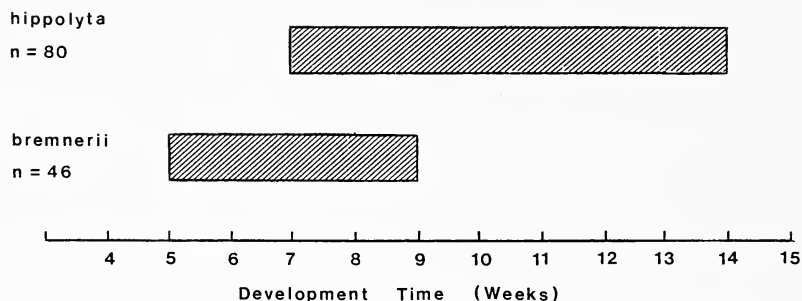


FIG. 4. Laboratory development time from first instar to adult in *S. zerene hippolyta* and *S. z. bremnerii* reared at  $22^{\circ} \pm 1^{\circ}\text{C}$ .

provide thermal advantages as well as cover from predators (McCorkle 1980). Some species may be mostly nocturnal (Dornfeld 1980:75). However, one field larva of *S. z. hippolyta* found during daytime in the present study was feeding, and laboratory larvae of many *Speyeria* feed both night and day. Their feeding is typically rapid so that they are exposed from cover only briefly. In the constantly heated laboratory, larvae probably grow faster than in nature. Their growth rate in the field may be delayed especially by cooler spring weather. Nevertheless, in the laboratory, they still required from one to three months to grow through six instars (Fig. 4, Table 1), and they spent about two weeks in the pupal stage.

Larval feeding signs were evident on violets in the Rock Creek meadow on 15 April 1980, indicating that at least some larvae were well into feeding activity. On 8 May 1986, one early 4th instar was observed. On 5 July, we found one nearly mature 6th instar (not parasitized) and several violets with fresh feeding signs, indicating that at least some larvae were still active. On the same date, however, the first adult male was taken, although normally the males do not begin to eclose until after 10 July with peak emergence in early August. Thus, the minimum natural larval feeding span is from mid-April to mid-June, some two months. It may be that a few larvae continue to feed well into August, producing the fresh adults present in early September.

### Pupa and Adult

The pupa (Fig. 2) is smooth, rounded, and mostly dark brown with variable paler areas on abdomen and wing covers, and a dark, transverse band on the anterior edge of each abdominal segment. As in most *Speyeria*, the pupal chamber consists of several leaves drawn together with silk, and the pupa is usually attached in a hanging position to the top of the chamber.

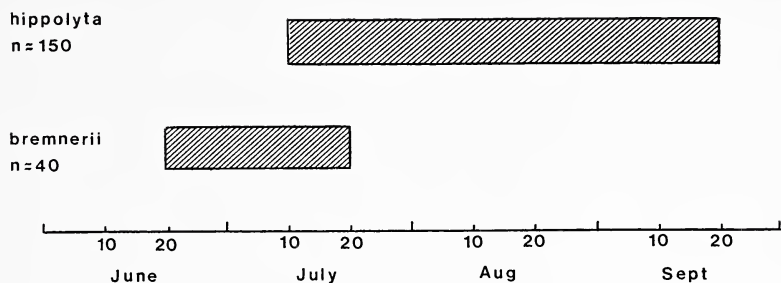


FIG. 5. Time range in field presence of fresh adults of *S. z. hippolyta* (central Oregon coast) and *S. z. bremnerii* (Willamette Valley).

As noted above, the first adult male was taken on 5 July, and a nearly mature larva was also found on that date. By early August, males were common (Fig. 5) (22 marked 1–3 August), and females had begun to appear (2 marked). Between 20 and 22 August, 22 new males and 7 new females were marked, including several fresh females and a few fresh males. On 4 September, 15 new males and 16 new females were marked. Of these, five females were fresh, three males were fairly fresh, and one very fresh. It is thus apparent that in this colony, males eclosed from mid-July until at least the end of August. The first females eclosed by the end of July, and eclosion continued through August to mid-September, with aging specimens surviving into October. Recapture results (McCorkle 1980) indicate that some adults live for at least three weeks, and disperse widely up to 2–3 km (1–2 miles). Butterflies fly inland and seek shelter along forest margins when strong winds are blowing off the ocean (McCorkle 1980).

#### ADAPTATIONS TO COASTAL ENVIRONMENT

Both coloration and wing size appear to have a strong genetic determination, since *S. z. hippolyta* differs consistently from the larger and paler Willamette Valley *S. z. bremnerii* both in the field and in laboratory rearings (Figs. 3, 6). The difference between forewing lengths (Fig. 6) is highly significant ( $P_t < 0.0001$ ). Data from Willamette Valley was obtained before the apparent extinction of these populations around 1977 (Hammond & McCorkle 1983).

There is evidence that small size and extensive dark basal suffusion as shown in *S. z. hippolyta* are adaptations to enhance solar heating, as would be needed in a marine-modified environment with persistent cold wind and frequent fog (McCorkle 1980). Butterflies, being heterothermic, usually depend on solar radiation to elevate body temperature sufficiently to allow flight necessary for foraging, mate seeking, escape from predators, and oviposition (Watt 1968, Douglas 1978,

TABLE 1. Time required for larval and pupal development in *Speyeria zerene* populations reared at 21–23°C. Each entry represents progeny of one female, with number of individuals in parentheses.

Subspecies	Locality	No. weeks	
		Males	Females
<i>bremnerii</i>	Benton Co., Oregon	6 (2)	7 (3)
		5–6 (5)	6 (5)
	Thurston Co., Washington	6–7 (3)	8–9 (3)
		6 (2)	7–8 (3)
<i>hippolyta</i>	Pacific Co., Washington	8–9 (3)	9–10 (5)
		8–9 (7)	9 (3)
	Clatsop Co., Oregon	7–9 (11)	8–10 (12)
	Lincoln Co., Oregon	8–9 (9)	9–10 (10)
	Lane Co., Oregon	7–9 (7)	8–10 (9)
<i>hippolyta</i> -like	Del Norte Co., California	9–13 (8)	12–14 (7)
		8–9 (5)	9–10 (7)
		10–13 (6)	11–13 (8)
<i>behrensi</i>	Curry Co., Oregon	7–8 (5)	8–9 (9)
		7–8 (2)	9 (5)
<i>gloriosa</i>	Josephine Co., Oregon	7–8 (11)	8–10 (12)
		7–8 (7)	9–10 (6)
<i>myrtleae</i>	Marin Co., California	7–8 (11)	8–10 (14)
		7–9 (11)	8–10 (10)
		8–9 (12)	8–10 (12)

McCorkle 1980). Rapid ovarian development is also thermodependent (Watt 1968).

*Speyeria* use a dorsal basking position in which the wings are extended in a horizontal plane from the body, thus exposing the dark basal suffusion to solar radiation. In dorsal basking butterflies, heat first absorbed by the basal part of the wings is then absorbed by the thorax, and usually a thick coat of long hairs serves as insulation for retention of thoracic heat (Douglas 1978, McCorkle 1980). Douglas (1978:43) suggests that large butterflies are at a disadvantage under cool conditions because they heat up more slowly, while smaller butterflies warm quickly to an adequate thoracic temperature. In a cold, windy environment, small butterflies also have a second advantage because the smaller wingspan allows flight closer to the ground where wind velocity is lower. Wind is a problem in maintaining body temperatures because heat is lost from the body surface by forced convection (Douglas 1978:69).

Since most *Speyeria* require high body temperatures for normal activity, they usually fly only in full sunshine, or under cloudy conditions when the air temperature is higher than 21°C (70°F). However, field observations of *S. z. hippolyta* revealed that it engages in normal activity under cloudy or foggy conditions with air temperatures as low as 16°C

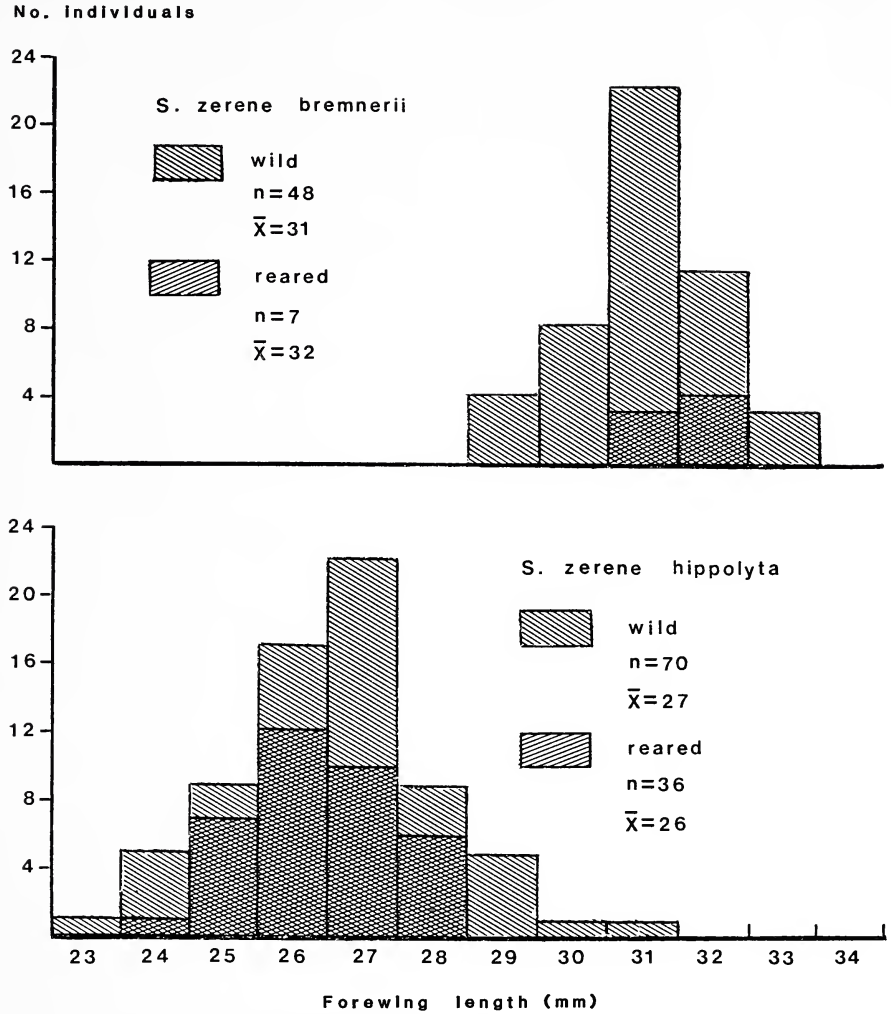


FIG. 6. Frequency distribution of male forewing length in wild and reared *S. zerene hippolyta* (central Oregon coast) and *S. z. bremnerii* (Willamette Valley).

(60°F), although the butterflies retreat to shelter under windy conditions. For example, during early September 1982, we observed approximately a dozen males in mate-searching flight, six males and females nectaring on flowers, and three females engaged in oviposition under windless, cloudy-foggy conditions with air temperature only 16°C (60°F). Similar observations have been made consistently during subsequent years. In sharp contrast, observations of the similarly colored *S. a. atlantis* (Edwards) in the Appalachians of West Virginia during 1977 revealed



virtually no evidence of similar activity under cool, cloudy conditions. These adults ( $N = 100+$ ) engaged in nectaring and flight only in full sunshine, and retreated to shelter in trees when clouds covered the sun at a temperature of approximately  $21^{\circ}\text{C}$  ( $70^{\circ}\text{F}$ ). In more dramatic contrast, the large *S. idalia* (Drury) favors minimum air temperatures of  $24\text{--}27^{\circ}\text{C}$  ( $75\text{--}80^{\circ}\text{F}$ ) for normal flight activities based on observations ( $N = 100+$ ) in Nebraska during 1983, and continues to fly at temperatures of  $41^{\circ}\text{C}$  ( $105^{\circ}\text{F}$ ) or more. This species exhibits little basking behavior in the field, and the basal wing areas completely lack dark suffusion. Even the black hindwings of *S. idalia* are mostly pale orange at the wing base.

Because *S. a. atlantis* and *S. zereue hippolyta* are nearly identical in their dark basal suffusion, and are of similar small size, the expected thermal regulation and behavioral activity of these species should be similar. Therefore, the above observations suggest that *S. z. hippolyta* employs an additional mechanism that allows activity under low temperatures and cloudy conditions. This mechanism might include changes in enzyme systems that would allow normal physiological function at low body temperatures, but this possibility has not yet been studied.

Finally, *S. z. hippolyta* along the central Oregon coast is also highly unusual in that adult emergence in the field extends over a long period of some 8 weeks from early July to early September, and it requires 7–14 weeks to complete larval and pupal development in the laboratory (Figs. 4, 5). These developmental patterns appear to be an additional adaptation to the coastal environment. By contrast, most western *Speyeria* emerge over a relatively short period of about three to four weeks in June and July. For example, the Willamette Valley form of *S. z. bremnerii* usually emerged during late June and early July in the field, and required only 5–9 weeks to complete larval and pupal development in the laboratory. As shown in Figs. 4 and 5, the sharp differences in the developmental patterns between *S. z. hippolyta* and *S. z. bremnerii* are maintained consistently both in field and laboratory, suggesting that a strong genetic component is involved.

There are two apparent reasons for these developmental patterns in *S. z. hippolyta*. In most years, adverse conditions of cold wind, fog, and rain persist along the ocean through May, June, and July, and weather more favorable for adult flight usually does not develop until August and September. The retarded larval development of *S. z. hippolyta* coordinates adult emergence with the best weather conditions in the coastal environment. In addition, adverse stormy weather may develop in some years along the coast during either August or September. The great range of individual variation in developmental rate and adult emergence suggests an additional adaptation to variable and un-

predictable weather conditions. Thus, early emerging butterflies may be more successful in reproduction one year, and late butterflies the next year, depending on each year's storm patterns. Since coastal weather is so variable from year to year, genes for both early and late emergence (fast and slow development) would tend to be maintained.

During the past 20 years, we have reared most of the geographic subspecies recognized in *Speyeria* under similar laboratory conditions at temperatures of 21–23°C (70–72°F). The fastest rate of larval and pupal development was observed in certain forms of *S. atlantis*, *S. egleis* (Behr), *S. callippe* (Boisduval), and Oregon *S. zerene bremnerii*, all of which required only five to six weeks for males and six to seven weeks for females. Most subspecies of *S. zerene* and *S. coronis* required six to seven weeks for males and seven to eight weeks for females. These include Sierran-type *S. z. zerene*, Rocky Mountain *S. z. sinope* dos Passos & Grey, and Great Basin *S. z. gunderi* (Comstock). Even very large-bodied species such as *S. c. cybele* (Fabricius), *S. idalia*, and *S. nokomis caerulea* (Holland) required only a similar amount of time, while *S. nokomis apacheana* (Skinner), *S. diana* (Cramer), and *S. edwardsii* required seven to eight weeks for males and eight weeks for females.

However, except for typical *S. z. bremnerii* itself, all populations of *S. zerene* within the *bremnerii* subspecies group as defined by Grey and Moeck (1962) exhibit a relatively long developmental time of 7–9 weeks for males and 8–10 weeks for females (Table 1). Our field emergence data (Fig. 5), indicate especially long and variable development times for *S. z. hippolyta* populations along the central Oregon coast from Lane Co. N to Tillamook Co.

Hammond & McCorkle (1983) noted *hippolyta*-like populations of *S. zerene* along the coast of Del Norte Co., California, N of Crescent City. These are disjunct from Oregon *hippolyta*, and are separated by intervening populations of an *S. z. behrensii-gloriosa* intergrade in Curry Co., Oregon. Two of three family lines reared from the Del Norte populations exhibited an extended development time of 10–13 weeks for males and 11–14 weeks for females (Table 1). Thus, the extremely variable developmental rates observed in field emergence of *S. z. hippolyta* are also seen in some family lines reared in the laboratory. In sharp contrast, two family lines of *S. z. behrensii* from Curry Co. to the north, and three family lines of *S. z. myrtilleae* from Marin Co., California to the south did not exhibit this extended development. Moreover, wild populations of *S. z. myrtilleae* usually emerge in the field during early to mid-July, a full month earlier than the *hippolyta*-like populations. The manner in which these emergence patterns relate to respective local weather is undocumented as yet.

There are two close parallels to *S. zerene hippolyta* within the Argynninae that also exhibit adaptations to cold, wet marine-modified grasslands. One is *S. mormonia bischoffi* (Edwards) in coastal S Alaska from the Kodiak region N to Anchorage. The second is *Fabriciana (Mesoacidalia) aglaja scotica* Watkins in the Hebrides and Orkney Islands N of Scotland. Both species display extensive dark suffusion over much of the dorsal wing surfaces. Ford (1945) indicated that *F. a. scotica* often exhibits reduced wing size on small, wind-swept islands.

In the San Francisco Bay area of California, both *Speyeria c. callippe* and *S. coronis coronis* also have heavy melanic basal suffusion in a cool, foggy coastal environment (Hovanitz 1941), although the California habitat is less severe compared to the northern coastal grasslands occupied by the previous three species.

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MARKING LEPIDOPTERA AND THEIR OFFSPRING:  
TRACE ELEMENT LABELLING OF *COLIAS EURYTHEME*  
(PIERIDAE) WITH RUBIDIUM

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**ABSTRACT.** Trace elements can be used to label lepidopteran eggs via treated adults, but sources and importance of sample variability are relatively unexplored. Female *Colias eurytheme* (Boisduval) reared on rubidium (Rb)-treated foodplants and their eggs were analyzed for Rb by atomic absorption spectrophotometry. Parent (3 untreated and 4 treated females) and mean egg (25/female) element content were significantly correlated. Compared with untreated adults and eggs, treated samples were reliably marked, although significant egg-to-egg variability in Rb concentration was found within and between sib-groups. Analysis-day differences were not significant. Adult sizes and element exposures may have contributed to between-group variance. Maternal and genetic influences were potential sources of within sib-group variance.

**Additional key words:** alfalfa butterfly, internal marker, adults, eggs, atomic absorption spectrophotometry.

Many methods for marking and monitoring lepidopteran populations have been proposed, tested, and employed with various degrees of success (Southwood 1978). An internal marking method that shows great potential for use in dispersal studies of phytophagous insects is that of trace element labelling (Berry et al. 1972). These labels can be used in concentrations low enough to permanently mark but not adversely affect the insect or its host. The mark can be acquired without handling the insect because it is obtained as the animal feeds on treated plant tissue (Stimmann et al. 1973) or nectaries (Culin & Alverson 1986). Insects in 7 orders, including 10 species of Lepidoptera in 5 families, have been successfully labelled (Hayes & Hopper 1987:table 1). Dispersal tests employing trace elements as adult markers have been conducted with three lepidopteran species: *Heliothis zea* (Boddie) and *Spodoptera frugiperda* (J. E. Smith) (both Noctuidae) (Graham et al. 1978); and *Pectinophora gossypiella* (Saunders) (Gelechiidae) (Van Steenwyk et al. 1978).

One recently revealed advantage of trace element use over external markers of Lepidoptera is that the mark is passed along to reproductive products, including eggs (Legg & Chiang 1984, Hayes & Hopper 1987) and spermatophores (Graham & Wolfenbarger 1977). Detection of a parental mark in the egg or spermatophore provides, much like a genetic marker, a potential means of assessing gene flow in the field. In measuring dispersal, recovery of eggs may prove superior to recovery of adults because the marked adult transmits multiple signals through the



distribution of marked eggs (Jones et al. 1980). Also, the possibility of using elemental marking of reproductive products in behavioral, physiological, or developmental studies is suggested, but has not been much explored (Engebretson & Mason 1981).

It remains to be seen whether recovery of marked eggs will prove feasible in large-scale field studies. However, the method has been used successfully to monitor small-scale egg dispersal by *Trichoplusia ni* (Hübner) (Geometridae) to adjacent crops (G. Ballmer pers. comm.). Among the many questions that need to be addressed is that of variability among eggs. Individual variability among adults can arise from exposure differences and differences in size or weight, and can occur through time. It has yet to be determined whether variability is passed along to offspring and whether there are intrinsic differences among eggs from the same female.

To investigate these areas and develop methods for more efficient and possibly expanded utilization of trace-element labelling, we analyzed marked adult *Colias eurytheme* (Boisduval) (Pieridae) and their eggs by atomic absorption spectrophotometry (AAS) for trace-element content. In addition to the parent-offspring relation, we examined egg-to-egg variability within sib-groups and among offspring of different parents. Differences between preparation dates were also considered possible sources of variability. Adult samples were prepared from bodies and head capsules and compared with egg samples to examine cost-effective adult sample preparation procedures.

#### MATERIALS AND METHODS

**Insects.** *Colias eurytheme*, the alfalfa butterfly, was used because of its tractability in the laboratory and greenhouse (Taylor et al. 1981), and because it is considered a model system for other Lepidoptera (Watt et al. 1974). Like *Heliothis* spp. and a number of other economically important Lepidoptera, *Colias* spp. are highly mobile, polyphagous, and distribute their eggs individually over a potentially large area (Tabashnik 1980). Experimental insects were obtained from a colony originating from eggs collected in November 1986 on commercial vetch, *Vicia villosa* Roth (Leguminosae), on the grounds of the Jamie Whitten Delta States Research Center, Stoneville, Mississippi.

**Treatments.** Adults were reared in the greenhouse from eggs or neonate larvae on vetch plants treated with rubidium (in chloride form). Host plants were grown from seed in vermiculite, and treated weekly with 1 g RbCl/l water (1000 ppm), initially by foliar application, then by watering the potting soil after insects were placed on the plants. Freshly treated host plants were provided as needed until pupation. Control insects were reared in a similar manner on untreated plants.

Treated and untreated pupae were placed in separate 2-l cardboard cartons with organdy top cloths and moistened paper towel liners. Eclosing adults were marked on the left hindwing with a felt tip pen (/ = treated; // = untreated), and placed in a mating cage. The cage, a  $0.6 \times 0.6 \times 0.3$ -m wood frame covered with transparent plastic, was provisioned daily with honey-water (1:3) soaked cotton balls, and held at 12°C without light. To stimulate mating, temperatures were elevated to 30°C and light was provided by two banks of fluorescent lights for 2–4 h/day. The cage was checked at 15–30-min intervals for the occurrence of mating. Pairs were removed and held at room temperature (ca. 25°C) until spermatophore transfer was completed. The males were uniquely marked and returned to the cage. For oviposition, females were placed individually on host plants covered by plastic bags and maintained at room temperature (ca. 25°C) and LD 12:12. Ovipositing females were fed daily with honey-water and transferred to fresh host plants as needed.

Twenty-five eggs from each treated female ( $N = 4$ ) and each untreated female ( $N = 3$ ) were collected separately by sib-group, and frozen. Eggs were obtained from day 1–2 of oviposition. When a female died, wings were removed and the body frozen.

**Sample digestion.** Individual eggs were digested, following the method of Hayes and Hopper (1987), by placing an egg directly into the sample cuvette along with 0.025 ml ultrapure nitric acid ( $\text{HNO}_3$ ), heating by microwave for 8–12 min at a low setting, and then diluting with 0.5 ml deionized distilled water (DDI).

The head and body of each female were placed in separate 7-ml scintillation vials with 0.2 ml and 0.4 ml ultrapure nitric acid, respectively. Digestion was allowed to occur at room temperature for 24 h, then samples were microwaved for 8–12 min. Digested material was then diluted with DDI, 4.0 and 5.0 ml, respectively.

**AAS analysis.** Samples were analyzed using a Perkin-Elmer 3030 with an HGA 400 graphite furnace and AS-40 autosampler. An electrodeless discharge lamp for Rb was used. Wavelength was set at 780 nm. Char and atomization temperatures were 800° and 1900°C (Slavin 1984). Elements were atomized off the wall of pyrolytically-coated graphite tubes.

**Data.** Initially, 10 eggs from each female (treated and untreated) were individually digested and analyzed by AAS for presence or absence of a detectable Rb signal (=day 1). To increase the sample size and examine between-analysis-day variability, an additional 15 eggs from each female were prepared and analyzed 14 days later (=day 2). To examine within-preparation variability, two separate aliquots of a single preparation from each head and body were decanted and analyzed on

different days. Mean values for head and body samples were used in subsequent analyses since no significant differences were found between dates (Mann-Whitney *U*-test).

Data were analyzed to determine reliability of mark detection for each female and her eggs. Mark thresholds for both eggs and adults (heads and bodies) were determined and compared by two methods: (1) using the high-range value of untreated controls, and (2) using the conservative method of Stimmann (1974), which assumes a normal distribution, three standard deviation units above the mean of untreated control samples. All Rb concentration values are given in units per egg or body part. Variation in egg weight within and between sib-groups was considered negligible for our purposes (mean dry wt = 0.111 mg, SE = 0.0017, N = 10/female). Variation in head and body weight was more extreme (mean dry wt of heads = 0.897 mg, SE = 0.1536; body wt = 16.54 mg, SE = 3.374). Within and between sib-group differences were examined by analysis of variance. Parent-offspring relation was evaluated by correlation of Rb content of a female body or head with the mean Rb content of her eggs. Data analyses were performed using SAS software.

## RESULTS AND DISCUSSION

The mean quantity of Rb (in ppm) found in the body, head capsule, and eggs of treated and untreated females is given in Table 1. Samples prepared from the bodies of treated females were found to be 100% reliably marked when compared to thresholds derived from samples prepared from untreated adults. However, only 10–20% of the samples prepared from heads alone produced detectable signals, and head results were not significantly correlated with body results ( $r = 0.30$ ). It is apparent that detectable quantities of Rb were not evenly distributed throughout the insect's tissues. The time and expense of digesting whole insects makes it advantageous to use the smallest sample that provides consistent results. For *Heliothis* spp. it has been found that a single wing is an adequate substitute for a whole moth (Hayes in press). For butterflies, the wing is not as practical because of large size and the frequent need to retain wings for morph determinations. Thus, *Colias* samples prepared from wingless and headless bodies were used, and they produced reliably detectable signals. If spermatophores are routinely dissected from females, or abdomens are removed for electrophoretic analysis, it would be ideal to be able to rely on a preparation from the thorax alone. However, a feasibility test for use of the thorax has not yet been conducted.

More than 90% of eggs (N = 100; 4 females) were determined to be detectably marked regardless of method used (92% exceeded range of

TABLE 1. Quantity of Rb (mean & range in ppm) in untreated and treated female *Colias eurytheme* (body and head) and their eggs (for 2 analysis days). Mark thresholds, both high range of untreated controls (Mark 1) and Stimmann value calculated from mean of controls (Mark 2), are provided along with mark determination (yes/no) or percentage of marks.

		Rb concentration			
Female no.	N	Mean	Range	Mark 1	Mark 2
Threshold values:					
Body	10			0.0185	0.0309
Head	10			0.0140	0.0213
Eggs (day 1)	30			0.0014	0.0015
(day 2)	45			0.0028	0.0026
Untreated					
1					
Body		0.0039 <sup>a</sup>		no	no
Head		0.0021 <sup>a</sup>		no	no
Eggs (day 1)	10	0.0004	0.0000–0.0012	0%	0%
(day 2)	15	0.0011	0.0003–0.0014	0%	0%
2					
Body		0.0182		no	no
Head		0.0046		no	no
Eggs (day 1)	10	0.0006	0.0002–0.0014	0%	0%
(day 2)	15	0.0013	0.0008–0.0022	0%	0%
3					
Body		0.0047		no	no
Head		0.0125		no	no
Eggs (day 1)	10	0.0002	0.0000–0.0006	0%	0%
(day 2)	15	0.0011	0.0004–0.0028	0%	0%
Treated					
4					
Body		0.0739		yes	yes
Head		0.0208		yes	no
Eggs (day 1)	10	0.0035	0.0011–0.0030	90%	80%
(day 2)	15	0.0038	0.0031–0.0048	100%	100%
5					
Body		0.0999		yes	yes
Head		0.0058		no	no
Eggs (day 1)	10	0.0035	0.0016–0.0160	100%	100%
(day 2)	15	0.0038	0.0030–0.0051	100%	100%
6					
Body	2	0.0378		yes	yes
Head	2	0.0106		no	no
Eggs (day 1)	10	0.0022	0.0011–0.0032	70%	70%
(day 2)	15	0.0045	0.0019–0.0077	73%	73%
7					
Body		0.0995		yes	yes
Head		0.0101		no	no
Eggs (day 1)	10	0.0063	0.0033–0.0169	100%	100%
(day 2)	15	0.0070	0.0049–0.0086	100%	100%

<sup>a</sup> Mean of two aliquots per sample; for further explanation see Materials and Methods.

nonmarks; 91% exceeded Stimmann's value). The proportion of detectably marked eggs per analysis day for each sib-group is given in Table 1. Significant correlation was found on both analysis days between maternal Rb content of the body and mean quantity of Rb in offspring (Table 1; day 1  $r = 0.88$ ,  $P < 0.01$ ; day 2  $r = 0.84$ ,  $P < 0.01$ ).

Analysis of variance revealed significant differences between treated and untreated samples ( $P < 0.0001$ ; Table 1). More than 60% of the variance was due to within-sib-group variance, more than 35% to between-group variance, and less than 1% was attributable to analysis-day variance. Low day-to-day analysis difference is reassuring because in field tests large numbers of samples must be processed over several days.

Between-group variance dropped to less than 20% for the untreated sib-groups when treated and untreated groups were analyzed separately. However, within-sib-group variance remained above 60%. Between-group differences could be attributed to differing insect sizes and element exposures. Eggs from a large female or one that has fed consistently on well-treated foliage may show higher levels of Rb than those from a smaller female or one that has fed inconsistently on a treated host plant.

Within-group differences cannot be understood as easily. Each female was mated only once, and use of the first eggs oviposited should lessen age effects. Since Rb is a potassium mimic, results suggest that the female does not supply her eggs with consistently similar quantities of necessary metabolites. Alternatively, inherent differences from egg to egg (genomic differences) may result in the observed Rb content variance. The parent-offspring correlation analysis reveals significant associations which may indicate some degree of inherent relation. Further investigation of these hypotheses could provide valuable insights into development, and might dictate an expanded role for the use of trace elements as an experimental tool.

In the final analysis, specimen-to-specimen, in particular egg-to-egg, variability does not present difficulties for use of this marking technique in field operations. Despite high individual variability, our findings indicate that labelled parents and offspring are readily distinguishable from unlabelled specimens.

Trace element marking has been reported previously with only one other butterfly species, *Pieris rapae* (L.), and then only in the adult stage (Stimmann 1974). The potential to exploit this marking method among all Lepidoptera is great. It seems well justified since mark-release-recapture studies using external markers are commonly used to study pest and nonpest lepidopteran population attributes (Ehrlich & Davidson 1960), but have received considerable criticism (Morton 1984).



Along with problems arising from handling insects, insufficient recapture numbers are a persistent problem. By labelling the egg, the adult signal is amplified, and the concomitant ability to directly assess gene flow is a definite advantage. Increasing the number of unique marks will also improve recapture efficiency per unit area. Along with Rb, other elements such as cesium and strontium are promising adult and possible egg markers.

#### ACKNOWLEDGMENTS

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## ANNOUNCEMENT

### JOURNAL COVER ILLUSTRATIONS AND FEATURE PHOTOGRAPHS

*Journal* submission categories are being broadened to include front cover illustrations and feature photographs. Submissions in these new categories, like all submissions to the *Journal*, may deal with any aspect of Lepidoptera study. Submissions in both categories must be accompanied by brief captions that include scientific names.

Cover illustration subjects are well depicted by past covers created before submissions were invited. Submissions should be no larger than letter size, with the caption for the inside front cover on a separate sheet. Drawings may be more suitable than photographs because drawings can usually better withstand the coarse reproduction necessitated by present cover stock texture. Submissions will be selected for artistry, novelty, and general appeal. There are no author page charges for cover illustrations.

Feature photographs might show unusual behaviors, unusual habitats, type localities, specimens in nature illustrating identifying marks, or other subjects. Photographic submissions should be mounted on white cardboard no larger than letter size, with a brief caption on a separate sheet. Feature photographs must be suitable for reduction to either half or full *Journal* pages (8.5 cm high by 11 cm wide, or 17 cm high by 11 cm wide, caption included). Submissions will be selected for photographic quality, scientific merit, and general appeal. Regular page charges will apply to accepted feature photographs.

Submissions in both new categories should be sent to the *Journal* editor.

WILLIAM E. MILLER, Editor

# AN APPRAISAL OF GAZORYCTRA HÜBNER (HEPIALIDAE) AND DESCRIPTION OF A NEW SPECIES FROM ARIZONA AND NEW MEXICO

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**ABSTRACT.** *Gazoryctra* includes 10 species from North America, and 3 from N Europe and Asia. Seven Nearctic species of *Hepialus* are transferred to *Gazoryctra*: *hyperboreus* Möschler, *lembertii* Dyar, *mathewi* H. Edwards, *novigannus* Barnes & Benjamin, *pulcher* Grote, *roseicaput* Neumoegen & Dyar, and *sciophanes* Ferguson. *Gazoryctra wielgusi* is described based on 94 males from the White Mountains of Arizona and adjacent New Mexico. A checklist of *Gazoryctra* is included.

**Additional key words:** *Gazoryctra wielgusi*, *Hepialus*, systematics, Holarctic.

*Gazoryctra* Hübner are medium-sized swift moths found in high latitudes or alpine habitats of the Holarctic Region. They are handsome moths, with brown, orange, or pinkish forewings and silvery white maculations. Adults of most species fly in late summer or fall. They are exceptionally strong fliers, particularly the diurnal arctic-alpine species. Many have very brief periods of diurnal activity, flying for only 20 or 30 min during evening twilight.

All previously known *Gazoryctra* were described in the nominotypical genus *Hepialus* Fabricius (or *Epialus* Lederer). North American *Gazoryctra* have been referred to as the "*hyperboreus* group" by Barnes and Benjamin (1926) and Ferguson (1979). Members of this group were incorrectly placed in *Phymatopus* Wallengren by Pfitzner (1912, 1937-38). Viette (1949) alone recognized that some Nearctic hepialids should be classified in *Gazoryctra*.

The purpose of this paper is to provide adult, pupal, and larval characters for the recognition of the genus, to clarify which elements of the Holarctic hepialid fauna belong to *Gazoryctra*, to validate nomenclature changes for the North American species, and to describe a new species from the southwestern United States.

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### Background

Hübner ([1820]:198) established three genera for the heterogeneous Palearctic swift moth fauna occurring in N Europe: *Gazoryctra*, *Pharmacis*, and *Triodia*. In his synopsis of the generic classification of European Hepialidae, Viette (1949) designated *Bombyx ganna* as type species of *Gazoryctra*. He characterized *Gazoryctra* as having a lobed valva and a toothlike trulleum in male genitalia, and further noted that small apical tibial spurs were present on middle and hind legs. He transferred to *Gazoryctra* the Palearctic *Hepialus macilentus* Eversmann and the Nearctic *H. confusus* H. Edwards and *H. mcglashani* H. Edwards. Later, Viette (1953) noted that *Gazoryctra* species also had prominent earlike lobes in the intersegmental membrane between abdominal segments 8 and 9 (socii of Robinson 1977, tergal lobes of Nielsen and Kristensen in press), and added a fifth species to the genus, *H. fuscoargenteus* Bang-Haas.

Many lepidopterists have overlooked or ignored the generic concepts of Hübner [1820], Wallengren (1869), Börner (1925), and Viette (1948, 1949), and have continued to treat most Holarctic swift moths as members of the nominotypical genus *Hepialus* (McDunnough 1939, Heath 1976, Ferguson 1979, Davis 1983). In North America, Hepialidae have been classified into two genera: *Hepialus* (type species: *humuli* Linnaeus) and *Sthenopsis* Packard (type species: *quadriguttatus* Packard). Most lepidopterists have recognized *Sthenopsis* from the time of its proposal in 1865 (Packard 1865, Kirby 1892, Neumoegen & Dyar 1894, Wagner & Pfitzner 1911, Forbes 1923, McDunnough 1939, Davis 1983). However, our studies indicate that *Hepialus humuli* and members of *Sthenopsis* (with *Zenophassus* Tindale, *Aenetus* Walker, and perhaps others) have a common ancestor not shared by most other Holarctic Hepialidae. Synapomorphies for these taxa include (1) a metatibial hairpencil in males; (2) swollen metatibiae in males (members of the *Sthenopsis regius* group and some *Aenetus* lack hairpencils and swollen metatibiae, but these appear to be reversals within the clade); (3) triangular forewings with falcate apices; (4) forewing scales with rounded apices; and (5) absence (loss) of the epiphysis in all but *Aenetus* and *Sthenopsis argenteomaculatus* (Harris). In addition, all members of this group are larger than most other Hepialidae and exoporian Lepidoptera, with forewing lengths typically exceeding 4 cm. Consequently, if *Sthenopsis* is to be retained as a distinct genus, then names proposed for more distantly related taxa like *Gazoryctra* warrant at least generic status.

### *Gazoryctra* in North America

So that we could reliably assign the hepialid described here to a genus, we prepared dissections of all the Holarctic hepialid generotypes.

We also examined all North American hepialid extant primary types, and prepared genitalia and wing slides for all named Nearctic and many European species, including all examined by Viette (1949).

In addition to the characters given by Viette (1949), eight others were found to be shared by *Gazoryctra* species: (1) forewing subcosta forked (vein Sc<sub>1</sub> well developed); (2) halves of tegumen meeting dorsoanteriorad, but free over much of midline; (3) dorsal margin of tegumen bearing dense oval patch of spinules; (4) caudal portion of trulleum not fused to tegumen; and (5) pulvilli large and setose. In the larva, (6) claw elongate, with basal tooth ending before ½; (7) D2 and SD setae on prothorax not grouped. In the pupa, (8) caudal band of teeth encircling abdominal segment 7 broken ventrolaterad.

Our studies indicate that *Gazoryctra* is the largest genus of North American Hepialidae. In addition to the two Nearctic species identified by Viette (1949), seven other described hepialids were found to share this list of characters and are transferred here to the genus *Gazoryctra*.

### Checklist

In what follows, subspecific names are indicated by a), and are but tentatively recognized. Author names followed by year do not necessarily refer to literature cited in this paper.

#### *Gazoryctra* Hübner [1820]

*Gazoryctes* Kirby 1892, missp.

*confusa* (H. Edwards 1884) (*Hepialus*)

*fuscoargentea* (Bang-Haas 1927) (*Hepialus*)

*sordida* (Nordstrom 1929) (*Hepialus*), infrasubsp.

a) *postmaculata* (Landin 1943) (*Hepialus*)

*ganna* (Hübner [1810]) (*Bombyx*)

*arctica* (Boheman 1848) (*Hepialus*)

*reducta* (Deutsch 1925) (*Hepialus*), infrasubsp.

*confluens* (Hellweger 1914) (*Hepialus*), infrasubsp.

*chishimana* (Matsumura 1931) (*Hepialus*), infrasubsp.

*hyperborea* (Möschler 1862) (*Epialus*), **new combination**

*lembertii* (Dyar 1894) (*Hepialus*), **new combination**

*macilenta* (Eversmann 1851) (*Hepialus*)

*gerda* (Staudinger 1897) (*Hepialus*)

a) *nesiotes* (Bryk 1942) (*Hepialus*)

*mathewi* (H. Edwards 1875) (*Epialus*), **new combination**

*matthewi* (H. Edwards 1884), missp.

*mcglashani* (H. Edwards 1887) (*Hepialus*)

*mcglachanii* (Pfitzner 1912), missp.

*noviganna* (Barnes & Benjamin 1926) (*Hepialus*), **new combination**

*novigana* (Pfitzner 1937-38) (*Hepialus*), missp.

a) *mackiei* (Barnes & Benjamin 1926) (*Hepialus*)

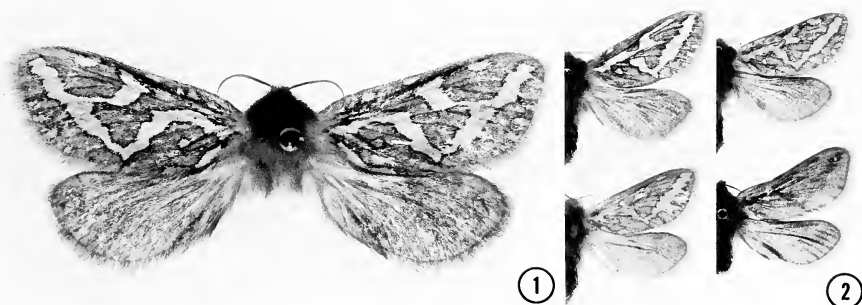
*pulchra* (Grote [1865]) (*Hepialus*), **new combination**

*roseicaput* (Neumoegen & Dyar 1893) (*Hepialus*), **new combination**

*mutata* (Barnes & Benjamin 1926) (*Hepialus*), infrasubsp.

*demitata* (Barnes & Benjamin 1926) (*Hepialus*), infrasubsp.





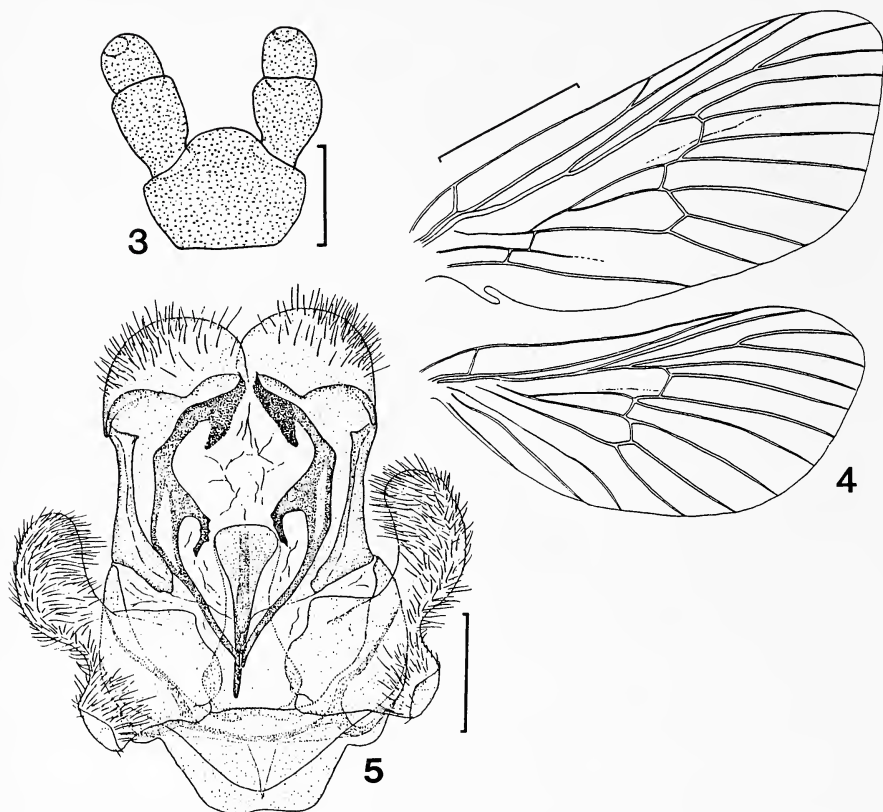
FIGS. 1, 2. *Gazoryctra wielgusi*. 1, Holotype male; 2, Paratype males from Ditch Camp. White scales replaced by silvery gray scales in lower right-hand specimen. Label data in text.

*sciophanes* (Ferguson 1979) (*Hepialus*), **new combination**  
*wielgusi* Wagner & Tindale, **new species**

### *Gazoryctra wielgusi*, new species

This pink and silvery moth is so far known only from a restricted area in the mountains of E Arizona and W New Mexico. Terminology for genital structures follows Birket-Smith (1974), Ueda (1978), and Nielsen and Robinson (1983); for wing veins, Nielsen and Robinson (1983); and for scale ultrastructure, Downey and Allyn (1975) and Kristensen (1978b).

**Male** (Figs. 1–11). Forewing length 15–18 mm (N = 94). **Head.** Antenna with 29–32 segments (N = 10), flagellomeres slightly compressed with abundant short setose sensory setae (Figs. 6, 7), yellow to orange-brown. Head vestiture dense admixture of buff and darker piliform scales; dark or dark-tipped scales prominent over frons, labial palpus, and ventral region. Labial palpus with 2 subequal segments (Fig. 3), vom Rath's organ dorsosubapical. **Thorax.** Pro- and mesothoracic dorsum with brown-tipped and buff piliform scales intermixed; metathorax buff. Procoxae and pro- and mesofemora dark-scaled. Tibiae and tarsi with elongate salmon-colored lamellar scales and contrasting dark fusiform scales (Fig. 8). **Venation** (Fig. 4).  $R_{2+3}$  branched at mid-length; hindwing vein CuP obscure in some specimens, and 2A differentiated from wing cuticle. **Scales** (dorsal surface over median region) (Figs. 10, 11). Broadest beyond middle, apices 3- or 4-toothed; secondary ridges prominent; windows small, circular to elliptical, diameter less than  $\frac{1}{5}$  interridge distance, surrounded by ring of unmodified cuticle, separated by 1 to 3 transverse flutes; window membrane occasionally present; flutes prominent with perpendicular secondary ribbing between adjacent flutes. Forewing tan or brown to peach or salmon with peppering of darker scales; heavily maculated with silvery white (rarely silvery gray) markings, these outwardly edged with dark scales; submarginal spots nearly always present, occasionally fused with oblique submarginal band; white spots or streaks also along subcosta and base of inner margin. Hindwing uniformly brown with orange or salmon-colored scales along margin, at apex, and extending basally along veins; apex faintly patterned. Fringe of both wings orange or salmon. **Abdomen.** Dorsum of segments 1 and 2 uniformly covered with long pale piliform scales; segments 3 to 8 with both long buff scales and lamellar salmon-colored scales. **Genitalia** (Fig. 5). Tergal lobes prominent, densely setose dorsad and laterad, hemispherical, with ventrolateral digitate lobe extending below margin of tegumen. Caudal margin of tegumen with 2 sets of ventrally projecting, strongly melanized processes, upper pair digitate and angled ventrad, apices with single prominent tooth and several smaller distal teeth; lower pair gradually tapering to



FIGS. 3-5. *Gazoryctra wielgusi*. 3, Labium: scale = 0.2 mm (DLW Slide 86-63); 4, Wing venation: scale = 0.5 cm (DLW Slide 86-62); 5, Male genitalia: scale = 0.5 mm.

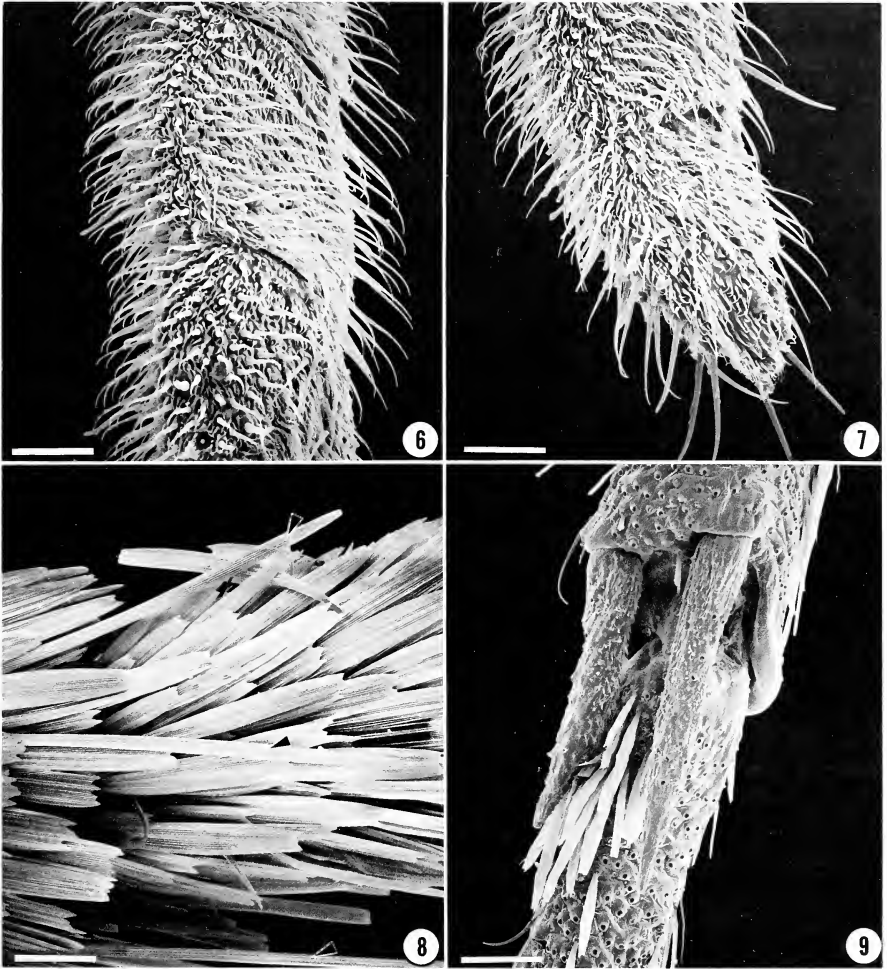
points, apices approximate over midline. Trulleum long, narrow, tapering to strongly melanized spine. Valva densely setose, boot-shaped; lower lobe rounded, curving mesad; inner margin notched above basal articulation. Juxta elongate, constricted in middle; roughly pentangulate. Vinculum often emarginate ventrolaterad.

**Female.** Unknown.

**Diagnosis.** A heavily maculated species with silvery white streaks and spots along base of inner margin, subcosta, and termen between medial veins. It can be readily separated from other strongly marked *Gazoryctra*—*confusa*, *hyperborea*, *pulchra*, and *roseicaput*—by its dark brown hind wings with contrasting orange or salmon-colored fringe. The oblique submarginal band is continuous, never broken into separate spots as is often the case in other members of the genus. It is the only salmon-colored *Gazoryctra* in the S Rocky Mountains. Male genitalic characters distinguishing *wielgusi* from at least some other members of the genus follow: tergal lobes nearly as high as broad, valva boot-shaped, vinculum ventrolaterally emarginate, trulleum very elongate.

**Distribution.** White Mountains of E Arizona and adjacent ranges in New Mexico between 2400 and 2800 m elev.

**Material examined.** 94 males. Holotype: Male, Arizona, Apache Co., 14.4 km E McNary, Ditch Camp, 2400 m, 25-VII-1974, R. S. Wielgus, at ultraviolet and white light, DLW Slide No. 86-66. Deposited in Los Angeles County Museum. Paratypes: Arizona: Apache

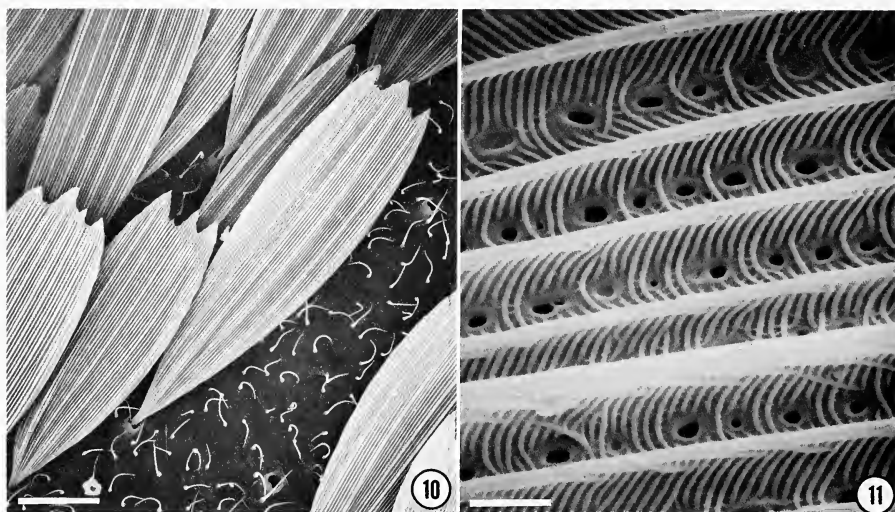


FIGS. 6–9. *Gazoryctra wielgusi* male. 6, Antenna showing abundance of sensory setae and cuticular projections. Scale = 43  $\mu\text{m}$ ; 7, Distal antennal segments. Scale = 43  $\mu\text{m}$ ; 8, Protibia. Fusiform scales (arrows) appear dark and spinelike against salmon-colored squamose scales. Scale = 60  $\mu\text{m}$ ; 9, Metathoracic tibial spurs. Scale = 100  $\mu\text{m}$ .

Co., same data as above, 25-VII/14-VIII-1974/80, R. S. Wielgus, 58 males (Fig. 2), and 26/29-VII-1978, N. B. & M. Tindale, 2 males; White Mtns., Greer, 2600 m, 4-VIII-1962, E. & I. Munroe, 4 males; Greer, 0.8 km S, Government Springs, 6-VIII-1977, R. S. Wielgus, 2 males, and 28/30-VII-1978, N. B. & M. Tindale, 10 males; Greer, 19.2 km SW, Winn Cmpgd., 2800 m, 26-VII-1986, R. Robertson, 12 males; Greenlee Co., Hannagan Meadow, "12-IV-1975", A. Menke, 3 males. New Mexico: Catron Co., Gila Wilderness, along route 78, Willow Creek Cmpgd., ca. 2400 m, 28-VII-1978, 1947 h MST, R. S. Wielgus, 1 male; Indian Creek nr. Gilita Cmpgd., 2400 m, 29-VII-1978, 1948 h MST, R. S. Wielgus, 1 male.

The three specimens of *G. wielgusi* in the USNM bearing the data "CALIFORNIA:





FIGS. 10, 11. *Gazoryctra wielgusi* scales from medial region of male forewing. 10, Scale showing typical exoporian arrangement of primary and secondary ridges. Scale = 30  $\mu$ m; 11, Scale ultrastructure: scutes and flutes well developed. Scale = 1.15  $\mu$ m.

Greenlee Co., Hannagan MDW., April 12, 1975, A. Menke" are mislabeled as there is no Greenlee Co., California. Moreover, all *Gazoryctra* species are summer- or fall-flyers. Presumably, Menke captured the moths in Hannagan Meadow during a collecting trip to the Southwest in August 1975 (A. Menke pers. comm.).

Paratypes are deposited at Arizona State University, Tempe; Australian National Insect Collection, Canberra; British Museum (Natural History), London; California Academy of Sciences, San Francisco; Canadian National Collection, Ottawa; Los Angeles County Museum, California; South Australian Museum, Adelaide; United States National Museum, Washington, D.C.; University of California, Berkeley and Davis; Zoologische Staatssammlung, Munich.

**Biology.** *Gazoryctra wielgusi* has a very brief period of adult activity. All specimens have been captured in early evening just after onset of darkness. In late July, the main flight occurs between 1945 and 2000 h MST (N = 17); by mid-August flight starts as early as 1930 h MST (N = 7). All specimens (males) were collected at light; typically they are the first moths to arrive at sheets. Adults are most numerous after afternoon rains and may even fly during strong rains (R. S. Wielgus pers. comm.).

Our records are from mesic areas in conifer forests. The locality at Ditch Camp is an open ponderosa pine forest with abundant grasses in open areas and nearby alders. Higher-elevation localities have more understory shrubbery. Spruce is dominant at the two sites in New Mexico. Nothing is known of the early stages. The larvae presumably are polyphagous, subterranean feeders, as are other Holarctic hepialids (Heath 1976, Wagner 1985, 1987). Recorded hosts for other *Gazoryctra* include *Betula*, *Phlox*, *Picea*, and grasses (Wagner 1985, Tham et al. 1985).

**Etymology.** We name this moth after Ronald S. Wielgus whose seemingly inexhaustible collecting efforts produced most of the known specimens and biological data.

## Discussion

*Gazoryctra* is confined to the Holarctic Region; 10 Nearctic and 3 Palearctic species are recognized. No member is recognized from both

faunas, although the markings of both *ganna* and *macilenta* approach those of *hyperborea* from North America.

*Gazoryctra* appears to represent one of the most primitive genera of Hepialidae. No synapomorphies have been identified that link *Gazoryctra* to other hepialids. In the past, the absence of tibial spurs has been used to define Hepialidae (Borror & White 1970, Kristensen 1978a, Nielsen & Robinson, 1983). Yet members of *Gazoryctra* possess a pair of small tibial spurs (Fig. 9, Viette 1949, Wagner 1985). In addition, the trulleum is free from the tegumen caudad in *Gazoryctra*, but fused in more derived Hepialidae (Nielsen & Scoble 1987).

Both adults and immature stages of *Gazoryctra* are rare in collections. Only three new hepialids have been described from North America since the turn of the century, and all belong to *Gazoryctra*. Moreover no specimens of *sciophanes* and *wielgusi* were known before 25 years ago. The biology is not known in detail for any species.

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## TEMPORAL TRENDS IN FREQUENCIES OF MELANIC MORPHS IN CRYPTIC MOTHS OF RURAL PENNSYLVANIA

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**ABSTRACT.** Five species of moths with recorded melanic forms were light-trapped for 10-16 years during 1971-86 at a remote mountain valley in E-central Pennsylvania. Observed melanic frequencies were: *Biston betularia cognataria* 0.52 (1971-78) and 0.38 (1979-86); *Epimecis hortoria* 0.34; *Phigalia titea* 0.14; *Charadra deridens* 0.64; *Catocala ultronia* 0.001. All but *Biston* showed constant melanic frequencies during their sampling periods.

**Additional key words:** Geometridae, Noctuidae, *Biston betularia cognataria*, *Lymantria dispar*.

Many eastern North American nocturnal moths that escape daytime predation by cryptic resting behavior have a moderate frequency of heritable dark forms. A simple working hypothesis to explain the adaptive advantage of this phenomenon is that these are "industrial melanics", favored by industrial and automotive pollutants in the atmosphere (Kettlewell 1973). Such an hypothesis is only vaguely supported in North America because of inadequate records. If trends showing systematic increases or decreases in frequency of melanics can be documented, the causes of such shifts might be found.

A second major body of relevant evidence results when enough localities are sampled for melanic frequencies. With these possibilities in view, I have been obtaining melanism data from daily light trap samples in a rural wooded valley for 16 years. The first eight years (1971-78) of records for *Biston betularia cognataria* (Guenée) (Geometridae) were presented and discussed previously (Manley 1981). In the present paper, data are given for *B. b. cognataria* for the next eight years (1979-86) as well as the first eight, and comparative records are included for *Epimecis hortoria* (F.), *Phigalia titea* (Cramer) (both Geometridae), *Charadra deridens* (Guenée), and *Catocala ultronia* (Hübner) (both Noctuidae). The observed melanic frequencies are compared with each other and with published records from other areas.

### MATERIALS AND METHODS

Sampling (dusk to dawn) was conducted nightly from April through early September each year using a fluorescent 15-watt blacklight and a mercury-vapor light trap. The trap was located in an isolated mountain valley 12 km NE of Klingerstown, Schuylkill Co., Pennsylvania. Except

TABLE 1. Melanic frequencies in four species of moths near Klingerstown, Pennsylvania. The two annual broods of *Biston betularia cognataria* are combined. Dash signifies no observation.

Year	<i>Biston b. cognataria</i>		<i>Charadra deridens</i>		<i>Epimecis hortoria</i>		<i>Phigalia titea</i>	
	Fre- quency	N	Fre- quency	N	Fre- quency	N	Fre- quency	N
1971	0.52	588	—	—	—	—	—	—
72	0.51	669	—	—	—	—	—	—
73	0.56	828	0.68	35	—	—	—	—
74	0.52	272	0.58	52	0.47	15	—	—
75	0.52	102	0.62	50	0.35	15	—	—
76	0.53	219	0.80	5	0.38	21	—	—
77	0.51	244	0.67	15	0.33	55	0.14	176
78	0.46	226	0.71	7	0.23	13	0.17	189
79	0.48	452	0.73	11	0.29	68	0.15	148
80	0.52	68	0.86	7	0.25	24	0.17	219
81	0.43	30	0	0	0.14	7	0.20	257
82	0.36	100	0	0	0.22	40	0.15	31
83	0.34	466	0	0	0.42	52	0.15	180
84	0.33	196	0.67	12	0.31	74	0.18	211
85	0.34	239	0.75	4	0.37	87	0.15	93
86	0.38	301	0.75	4	0.38	60	0.10	33
Total	0.47	5000	0.65	202	0.33	531	0.15	1537

for a few open fields, the area is tree-covered. Details of site, sampling methods, and regional sources of air pollution potentially affecting air quality and melanic frequency are given in Manley (1981). Sampling extended over a period of 10 or more years for each species. Specimens were pinned with full data and are part of the Manley Collection, Peabody Museum of Natural History, Yale University.

The data format in Table 1 allows quick comparisons with Owen (1961, 1962), Sargent (1971, 1974), and Klots (1964, 1968). *G*-tests using Williams's correction (Sokal & Rohlf 1981) were employed to test whether melanic frequencies differed from year to year.

## RESULTS

*Biston betularia cognataria* appears to undergo large fluctuations in population density every 4–5 years (Table 1). In 1975, the first brood consisted of 3 trapped specimens followed by a second brood of 99, with the melanic frequency of 0.52 equal to the first 8-year average (Manley 1981). The melanic frequency declined from 0.52 in 1980 to 0.33 in 1984, while numbers trapped rebounded to levels before the population crash of 1980–81. Populations after 1981 show a six-year (1981–86) melanic frequency of 0.34, compared to 0.48 for the 6-year period (1975–80) following the 1975 crash. This contrasts with a frequency of 0.53 for the first 4 years (1971–74).

The 1971–78 trends in *Biston b. cognataria* were earlier interpreted

partly as a gradual decline in melanic frequency (Manley 1981). The new data here strengthen this suggestion (linear regression of melanic frequency against year: slope =  $-0.016 \pm 0.002$ ,  $N = 16$ ,  $t = 7.27$ ,  $P < 0.001$ ). However, an equally plausible explanation is the population crash of 1981 (1971–80 data versus 1981–86 data:  $G = 132.47$ ,  $df = 1$ ,  $P < 0.001$ ; samples in 1971–80 set are homogeneous, as are samples in 1981–86 set,  $P > 0.25$  by  $G$ -tests).

*Epimecis hortoria* (Table 1) exhibits a stable frequency of 0.33 for its melanic form “*carbonaria*” ( $G = 9.98$ ,  $df = 12$ ,  $P > 0.50$ ). This moth has become increasingly abundant at the light trap since its population crash in 1981. Owen (1961, 1962) reported a 1957 sample of 8 specimens from Westmoreland Co., just E of Pittsburgh, as 100% melanic, and a 1959 sample at Lebanon, Hunterdon Co., New Jersey, as 0.90.

The melanic form “*deplorens*” of *Phigalia titea* is distinct, with no apparent intermediates; it (Table 1) maintained a stable frequency of 0.15 during the sampling period ( $G = 3.66$ ,  $df = 9$ ,  $P > 0.50$ ). Owen (1961) reported 1960 melanic frequencies in Michigan ranging from 0.11 to 0.14; Sargent (1971) reported 1968–70 melanic frequencies at Leverett, Massachusetts, at 0.20.

My samples of *Phigalia titea* were taken 25 March through 5 May. Since this moth begins flying on warm March nights, a portion of the total possible sample of it was probably not taken. My samples reflect only warm nights in late March with no continuous sampling until April. Nevertheless, there does not appear to be substantive change in melanic frequency of this species.

Melanic frequency for *Charadra deridens* during 1973–86 (Table 1) was stable at 0.65 ( $G = 3.89$ ,  $df = 9$ ,  $P > 0.50$ ). Klots (1968) at Putman, Windham Co., Connecticut, reported limited 1961–66 samples ( $N = 28$ ) to be 0.89 melanic, and a laboratory reared sample ( $N = 39$ ) to be 2:1 melanic.

*Charadra deridens* samples have been small since 1981–83, when no moths were taken (Table 1). The 10-year melanic frequency of 0.65 is the highest of any melanic moth sampled to date at this locality.

*Catocala ultronia*, the most abundant *Catocala* in central Pennsylvania, was sampled during 1968–78. In my sampling, only 2 of 1520 specimens were the melanic form “*nigrescens*”, all others being color variants of form “*celia*”. Sargent (1974) reported the 1968–74 melanic frequency in Leverett, Massachusetts, to be 0.17 ( $N = 586$ ).

#### DISCUSSION

Except for *Catocala ultronia*, the species discussed in this paper show strong melanic tendencies. Melanic frequencies differ from those observed at Leverett, Massachusetts (Sargent 1974), even for the same

years. Melanic frequency appears to fluctuate independently at least in part among species. Some factors affecting melanic frequencies are presented in Manley (1981).

The 1980–81 season heralded severe reductions in the populations of *Biston*, *Epimecis* and *Charadra*, whereas *Phigalia* produced the largest sample of its 10-year period, only to be reduced to 31 individuals in 1982. An explanation for the sudden reductions in population densities could in part be local infestation of the deciduous woods by the gypsy moth, *Lymantria dispar* (L.). A partial defoliation in 1980 was followed by severe defoliation in 1981 and aerial spraying with Dylox or Dimilin by the Pennsylvania Department of Forestry. Spraying was discontinued in 1982, and no noticeable defoliation has occurred since.

Four species in this study are polyphagous. More than 50 species of trees and shrubs are recorded for *Biston betularia cognitaria*, with *Salix*, *Populus*, *Betula*, and *Alnus* preferred (Rindge 1975, McGuffin 1977). Prentice (1963) lists 25 species of hard and softwoods for *Phigalia titea*, with *Tilia*, *Ulmus*, *Betula*, *Populus*, *Acer*, and *Quercus* preferred. *Epimecis hortoria* prefers *Liriodendron*, *Sassafras*, and *Prunus*, and is rarely found on other deciduous trees (Forbes 1948). *Charadra deridens* prefers *Ulmus*, *Betula*, and *Quercus* (Forbes 1954). Only *Quercus* among the preferred food plants is normally eaten by the gypsy moth. Aerial spraying to control gypsy moth may have been a critical factor in reducing populations of the polyphagous species. The rapid recovery of *Biston* and *Phigalia* following reductions in 1981–82 (Table 1) could be attributed to the wide range of food plants acceptable to these species. Similarly, the preferred food plants of *Epimecis* are not those eaten by larvae of the other species in this study, thus perhaps accounting for a rapid recovery in 1982. *Charadra deridens*, a *Quercus* feeder (Forbes 1954), appears to have been severely reduced in the defoliated area, as none were trapped from 1981 to 1983, and it remains rare in the area (Table 1).

The population reduction of *Phigalia* in 1982 does not coincide with the 1981 reductions of the other species (Table 1) in that the annual sample was taken before the aerial spraying in 1981.

Defoliation by gypsy moth opens the forest canopy, allowing light penetration which could aid predators in finding active adults, especially ovipositing females. The tendency of birds to seek the safety of trees escaping defoliation could increase the density of predators on larvae feeding on those trees, as well as on ovipositing females.

Air pollution over Pennsylvania is often from industrial areas in the Ohio Valley and Gulf Coast (Brown 1987). Local sources of pollution do not greatly increase the quantity of oxides of sulfur and nitrogen in the sampling area, since the area is not industrial. Despite reports of a



two- to three-fold increase in ozone and other oxidants in the Appalachians between 1962 and 1976 (West 1977), air pollution may not be a critical factor in fluctuations in melanic frequencies at this site. Despite high levels of polluted air over Pennsylvania, four of the five species sampled in this report have stable melanic frequencies. The determining factors appear to be localized biological factors, like gypsy moth.

The data here suggest that the widespread aerial spraying for gypsy moth control may be having a catastrophic effect on many species of lepidopterous insects in the eastern United States.

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A NEW SPECIES OF *OCALARIA*  
(NOCTUIDAE: CATOCALINAE) AND ANALYSIS OF  
SOME MORPHOLOGICAL CHARACTERS USEFUL  
FOR ELUCIDATING NOCTUID PHYLOGENY

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**ABSTRACT.** *Ocalaria cohabita* is described from 24 specimens captured on Barro Colorado Island, Panama. A key to adults of *Ocalaria* is provided, followed by a morphological comparison of *O. cohabita*, *O. oculata* (Druce) and *O. quadriocellata* (Walker). Particular emphasis is placed on characters that may prove useful in elucidating noctuid phylogeny, including features of head, legs, wings, abdominal segments 2 and 8, and genitalia.

**Additional key words:** morphology, Panama, *Ocalaria oculata*, *O. quadriocellata*, systematics.

Greig and DeVries (1986) described the gregarious diurnal roosting behavior of a small noctuid moth from Parque Nacional Corcovado in Costa Rica. This moth was an undescribed species of *Ocalaria* Schaus. Adults of this species were subsequently captured near the Smithsonian Tropical Research Institute on Barro Colorado Island, Panama, and sent to me for identification. Comparison with illustrations of Corcovado specimens showed that the Panamanian material was conspecific. The species is described below.

*Ocalaria cohabita*, new species  
(Figs. 1-5, 10, 14, 16, 17, 20, 21, 24, 26)

**Diagnosis.** Forewing underside discal eyespot with double pupil, smaller pupil surrounded by iridescent deep-blue scales, lacking marginal blue-green scales; hindwing underside with solid brown band between postmedian and subterminal lines; male antenna serrate.

**Male. Head.** Haustellum unscaled; labial palp mainly dark gray-brown, first segment with some off-white scales dorsally and lateroventrally, smooth-scaled laterally but scales on dorsal and ventral edges projecting as a loose fringe, 2nd and 3rd segments uniformly dark gray-brown, smooth-scaled on all surfaces, subequal in length, elongate, ascending in life, at rest recurved dorsally over head (Greig & DeVries 1986:fig. 4), 2nd segment gibbous; antenna long, almost equal to forewing length, dorsally uniformly scaled dark gray-brown, ventrally serrate, sensory setae distinct, white; eyes large, bulbous, bare, unlashd; frons narrow, unscaled on lower half except for extreme edges, scales on dorsal half projecting anteriorly forming median ridge; frons, vertex, occiput dark gray-brown except for band of off-white scales bordering eye posteriorly. **Thorax.** Patagia, thoracic scaling concolorous with head, tegulae similar but with weak, transverse, median white band. **Legs.** All uniformly dark gray-brown dorsally, off-white ventrally; apices of tibial and tarsal segments off-white, weakly so on forelegs, more strongly marked on hindlegs; tibiae unspined. **Forewing length** 13.4-16.0 mm (holotype 16.0 mm). **Wings** (Figs. 1, 2). Forewing ground color dark gray-brown, transverse bands pale gray, with weak purple

iridescence in oblique lighting; space on forewing enclosed by costa, discal cell, antemedian line pale orange; eyespot black with off-center white pupil, surrounded by ring of pale orange; apical spot black with basal small white spot; ventral pattern similar to upper but more colorful; forewing pale gray, ventral of discal cell as far as postmedian line, eyespot as upper surface but with additional smaller white pupil posterodistal to main pupil, smaller pupil surrounded by deep blue iridescent scales visible only in oblique lighting, area between postmedian and subterminal lines violet-gray with central brown area, anterior part suffused with orange scales; pupil of apical eyespot much larger than on upper surface, rounded or square, subequal to main pupil of discal eyespot; distally veins  $R_5$  and  $M_1$ , together with costal area to apical eyespot, orange; hindwing ground color pale gray, suffused costally with brown scales, discal lunule, antemedian, postmedian, and subterminal lines dark gray-brown, distinct; brown band present between postmedian and subterminal lines, bounded basally and distally by pale gray. **Abdomen.** Dorsally and ventrally transversely striped, anterior half of each segment pale gray, posterior half dark gray-brown. **Genitalia** (Fig. 3). Uncus with small apical hook; saccus ovoid; juxta ill-defined; valve simple, lacking appendages, with a strong constriction on the costa basally; aedeagus cylindrical, with bluntly-pointed apical process; vesica without cornuti.

**Female.** As described for male except antenna filiform, wings broader, more rounded, not as acutely pointed (Figs. 1, 2). Ratio of forewing length to maximum width perpendicular to costa averaging 2.28 in males ( $n = 12$ ) and 2.11 in females ( $n = 11$ ), the 0.17 difference being significant ( $P = 0.001$ , 1-tailed Mann-Whitney test because larger ratio expected in males). **Genitalia** (Fig. 4). Segment 8 annular; antrum membranous, undifferentiated from ductus bursae; corpus bursae membranous, ovoid, lacking signa; ductus seminalis broader than ductus bursae, arising from posterior end of corpus bursae.

**Types.** Holotype male: Panama, Barro Colorado Island, 20 May 1986, N. Greig. Paratypes: 1 female: Panama, Barro Colorado Island, 28 May 1986, P. J. DeVries (BMNH noctuid slide #12816); 11 males, 11 females: Panama, Barro Colorado Island, 18 August 1986, P. J. DeVries (BMNH noctuid slides #12803–12815). In British Museum (Natural History).

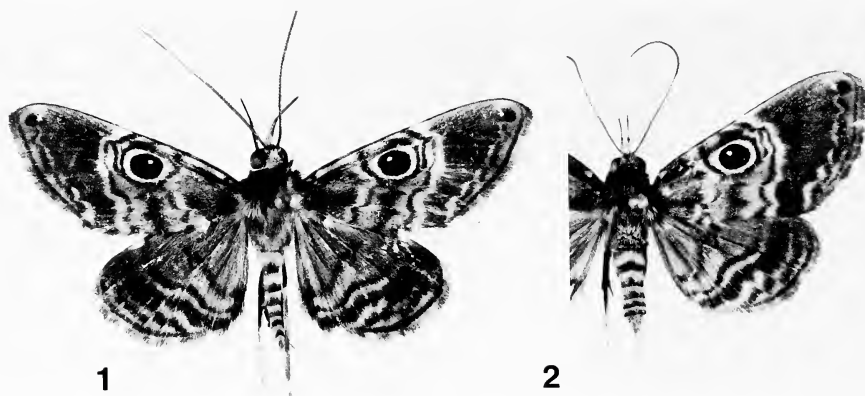
**Life history.** Nothing is known about the immature stages or larval hosts of any species of *Ocalaria*.

**Variation.** There is no major variation in wing pattern either between or within sexes. The pale orange forewing costal band may be weakly subdivided medially by ground color scales. However, older moths become worn and faded, eventually presenting a "washed-out" pale coloration. This phenomenon affects wings and body scales equally and appears due to a combination of scale loss and fading of brown pigments.

### Key to Adults of *Ocalaria*

*Ocalaria* currently contains 7 described species (provenances and numbers examined are those of specimens held in BMNH): *dioptrica* (Walker) (= *macrops* (Felder & Rogenhofer)) (Brazil: Amazonas,  $n = 2$ ; Peru: Amazonas,  $n = 1$ ; Bolivia,  $n = 2$ ; French Guiana,  $n = 1$ ), *guarana* Schaus (Brazil: Rio de Janeiro,  $n = 2$ ; São Paulo,  $n = 1$ ), *oculata* (Druce) (Guatemala: San Isidro,  $n = 56$ ), *pavina* Schaus (Brazil: Rio de Janeiro,  $n = 9$ ), *pavo* Schaus (Costa Rica: Sixola), *quadriocellata* (Walker) (Brazil: Cuiabá,  $n = 11$ ) and *cohabita*, new species.

The couplet for *O. pavo* is based on a small water-color painting in BMNH, which lacks specimens of this species. This type of painting, probably commissioned by G. F. Hampson, has been found to be realistic and reliable as an identification guide (A. Watson pers. comm.).



FIGS. 1, 2. *Ocalaria cohabita*. 1, Holotype male; 2, Paratype female.

1. Discal eyespot on forewing underside with single white pupil (occasionally double in *O. quadriocellata*, not surrounded by deep blue iridescence), marginal iridescent blue-green scales; hindwing underside without solid brown band between postmedian and subterminal lines; male antenna bipectinate ..... 2
- Discal eyespot on forewing underside with double pupil, smaller pupil surrounded by iridescent deep blue scales, lacking marginal blue-green iridescence; hindwing underside with solid brown band between postmedian and subterminal lines; male antenna serrate ..... *cohabita*, new species
2. Area between postmedian and subterminal lines on upperside of both wings solid dark brown, edged with continuous pale cream lines ..... *pavo* Schaus
- Area between postmedian, subterminal lines on upperside of both wings not solid dark brown, pale line bordering inner edge of subterminal line interrupted ..... 3
3. Discal eyespot on forewing upperside subequal to apical eyespot; brown streak present in discal fold between median and postmedian lines ..... *pavina* Schaus
- Discal eyespot on forewing upperside much larger than apical eyespot; brown streak in discal fold between median, postmedian lines absent ..... 4
4. Forewing upperside, distal to discal eyespot, with conspicuous white spot often divided in half by brown scaling along vein  $M_3$  ..... *quadriocellata* Walker
- Forewing upperside without such spot ..... 5
5. Forewing underside with white spot or streak below apical eyespot; pupil of apical eyespot small, no more than half width of eyespot in diameter, surrounding black scales conspicuous ..... 6
- Forewing underside without white spot or streak below apical eyespot; pupil of apical eyespot large, subequal in diameter to width of eyespot, almost obliterating surrounding ring of black scales ..... *oculata* Druce
6. Ground color dark brown; forewing upperside postmedian line cream, continuous across wing; discal eyespot on forewing underside without diagonal cream line below ..... *guarana* Schaus
- Ground color off-white suffused with pale brown; forewing upperside postmedian line indistinct, not continuous across wing; discal eyespot on forewing underside with diagonal cream line below, originating from posterobasal corner of the eyespot ..... *dioptica* Walker

### Comparative Morphology of *O. cohabita*, *O. oculata*, and *O. quadriocellata*

In a previous cladistic analysis of Plusiinae (Kitching 1987), I described several characters useful in elucidating generic and higher level

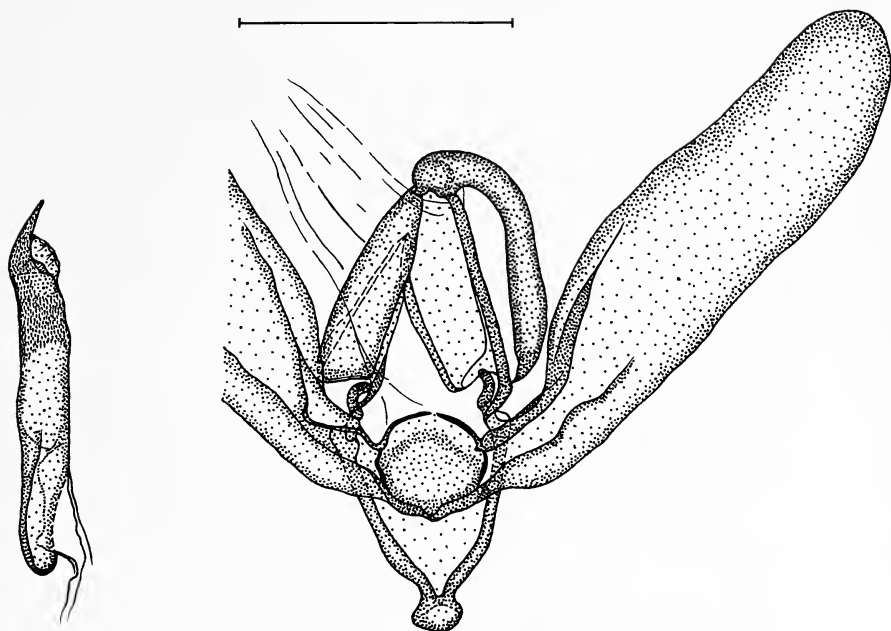


FIG. 3. *Ocalaria cohabita*, paratype male genitalia, BMNH noctuid slide #12804 (genitalia) and #12805 (aedeagus). Scale line = 1 mm.

interrelations on the proboscis, female frenulum, basal abdominal segments and abdominal segment 8. I have examined these structures in three *Ocalaria* (*O. cohabita*, *O. oculata* and *O. quadriocellata*) and here describe the results to facilitate future analyses of higher classification of Catocalinae. *Ocalaria oculata* and *O. quadriocellata* were chosen for detailed examination because they are well represented in the BMNH collection; the remaining species (several undescribed) were not because it was not my intention to revise the genus. Comparisons are also drawn, where appropriate, with equivalent conditions in Plusiinae and the taxa employed as outgroups in that study.

**Labial palps.** In all three *Ocalaria* species, the dorsal margin of segment 2 of the labial palp is markedly convex. This feature is more conspicuous in *O. quadriocellata* (Fig. 6) and *O. oculata* than in *O. cohabita* (Fig. 5) but there is no sexual dimorphism. The function of the bulge is unknown; examination at 400 $\times$  revealed no obvious sensory structures or differential scale arrangements.

**Antennae.** Female *O. cohabita* have filiform antennae (Fig. 16) with relatively short subventral setae; males have longer, more conspicuous subventral setae, while the ventral surface of each segment is produced into a rounded triangular flange (Fig. 14), giving a serrate appearance



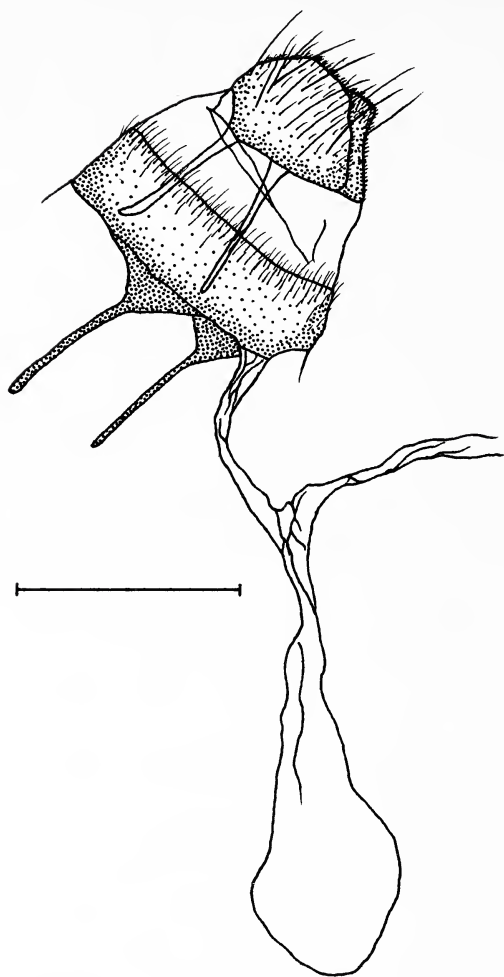
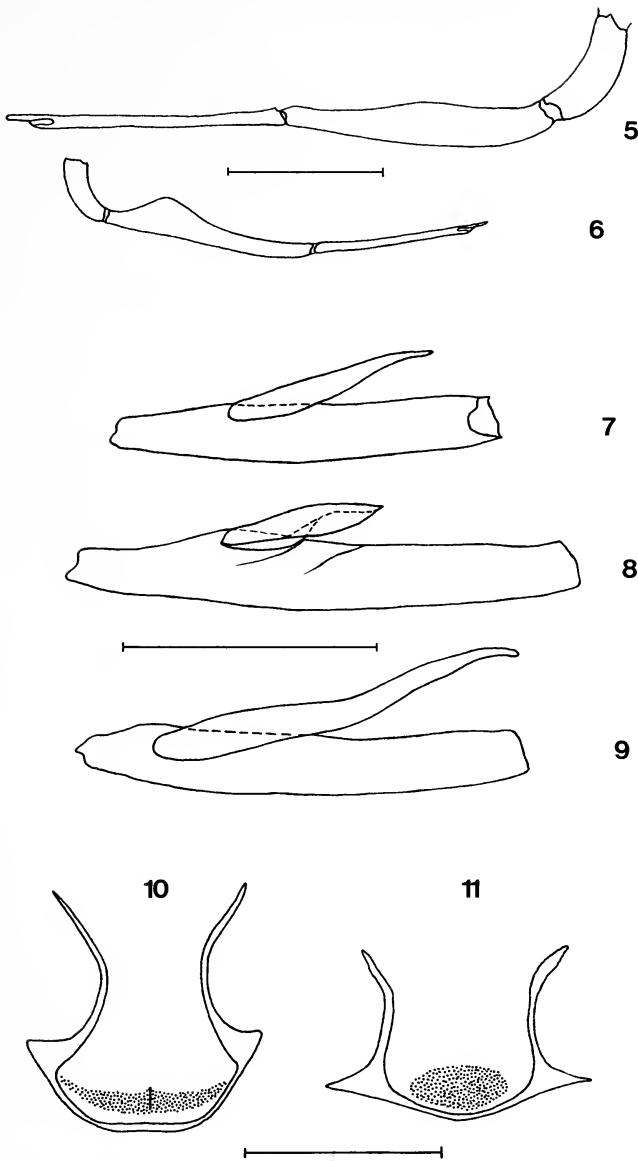


FIG. 4. *Ocalaria cohabita*, paratype female genitalia, BMNH noctuid slide #12816. Scale line = 1 mm.

to the antenna. Apically, this flange bears two setae and a sensillum styloconicum.

Antennae of female *O. quadriocellata* are also filiform, although the segments are longer than in *O. cohabita*. In contrast, male antennae of *O. quadriocellata* are strongly bipectinate (Fig. 12). Each pair of pectinations, which arise at the base of a segment, are long, slender, parallel-sided and bear a strong apical seta. Male *O. oculata* are similar but the pectinations are even longer and thinner (Fig. 15). Female *O. oculata* are unique among the three taxa studied in also having bipectinate



FIGS. 5-11. *Ocalaria* structures. 5, 6. Labial palps. 5, *O. cohabita* male; 6, *O. oculata* female. 7-9. Foretibiae. 7, *O. oculata* female; 8, *O. quadriocellata* female; 9, *O. oculata* male. 10, 11. Male sternite 8. 10, *O. cohabita*; 11, *O. quadriocellata*. Stippling indicates extent of hairpencil scale insertions. Scale lines = 1 mm.

antennae (Fig. 13), although the branches are shorter than in either male *O. oculata* or *O. quadriocellata*.

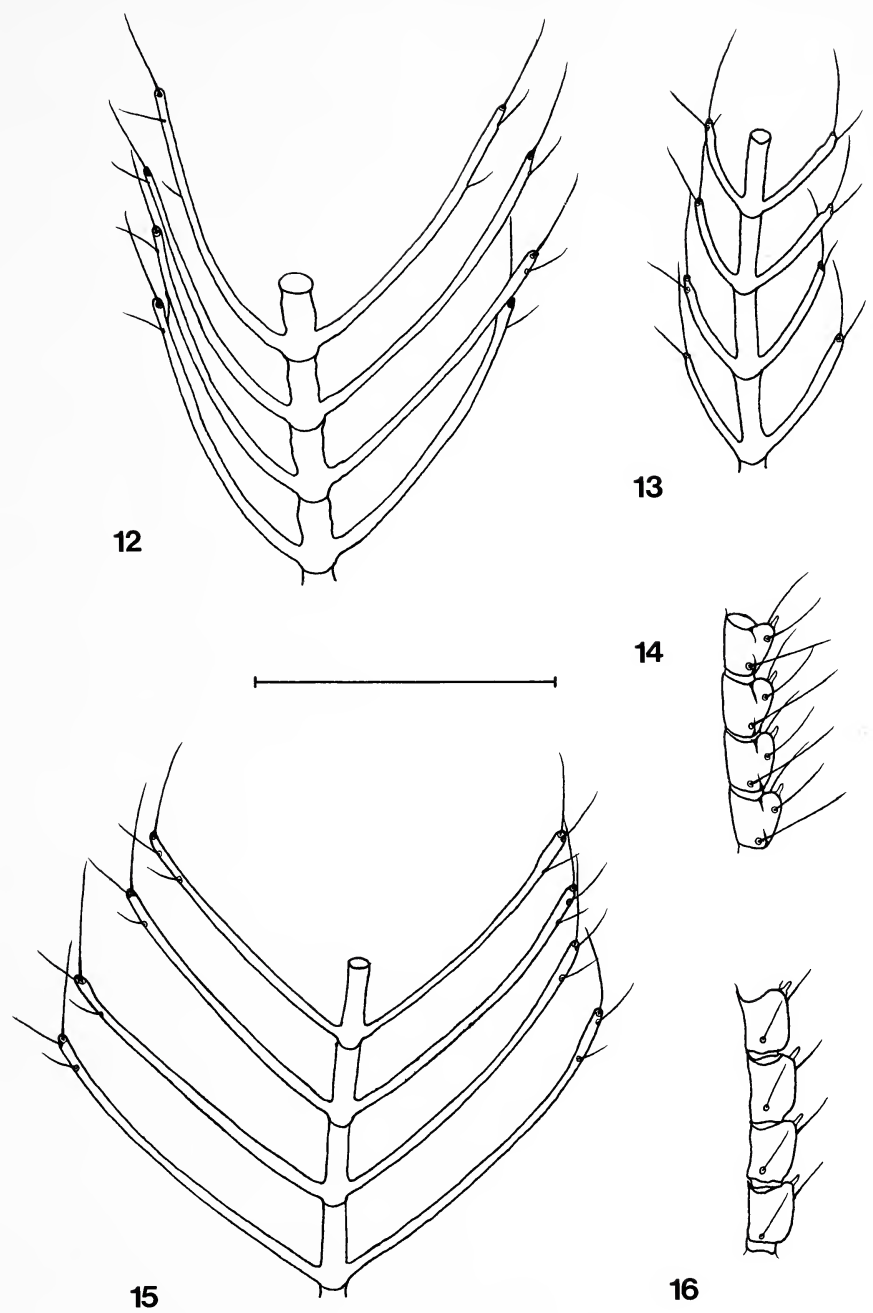
**Proboscis.** Proboscides in all three species are short, stout, and similar in general appearance to those of such genera as *Oncocnemis* Lederer (Cuculliinae), *Magusa* Walker (Amphipyridae), *Stictoptera* Guenée (Stictopterinae) and *Paectes* Hübner (Euteliinae). *Ocalaria* also shares with these and other genera a nodular apex to the proboscis and ridged styloconic sensilla (which appear stellate in apical view), all of which suggests that this form of proboscis is plesiomorphic within Noctuidae. Concomitantly, the form of proboscis found in Plusiinae is apomorphic for that subfamily, although certain features appear to have been convergently derived in *Cucullia* Schrank and *Calophasia* Stephens (both Cuculliinae).

**Epiphysis.** The epiphysis in *Ocalaria* exhibits considerable variation in length. In both sexes of *O. cohabita* and female *O. quadriocellata*, it is small, being only about a quarter the length of the fore-tibia (Fig. 8). However, in male *O. quadriocellata* and *O. oculata*, the epiphysis is highly elongate and often exceeds the fore-tibial apex (Fig. 9). Female *O. oculata*, which have smaller antennal pectinations, also have a shorter epiphysis, but one that is still elongate compared to female *O. cohabita* (Fig. 7). This close correlation between epiphysis length and degree of development of antennal pectinations is strong circumstantial evidence to support the hypothesis that the primary role of the epiphysis is keeping the antenna clean. A long epiphysis is necessary in male *O. quadriocellata* and *O. oculata* to clean the long pectinations efficiently.

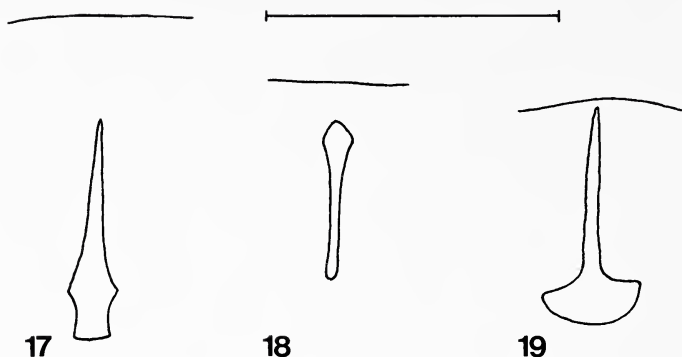
**Wings.** Venation of *Ocalaria* is typical quadrifine noctuid, although hindwing vein  $M_2$  is somewhat weaker than either  $M_1$  or  $M_3$  and does not arise close to the base of  $M_3$ . A potential *Ocalaria* apomorphy in hindwing shape is the shallow concavity just beyond the midpoint of the costal margin, although this is weakly expressed in *O. oculata*. All *Ocalaria* examined have a trisetose female frenulum in which the setae are subequal in length, further corroborating the hypothesis that this state is plesiomorphic within Noctuidae (Kitching 1987).

**Abdominal segment 2.** In all noctuid genera examined so far, the anterior edge of tergite 2 (T2) bears an inflected flange. At its simplest, the flange is concave, uniformly narrow and difficult to discern in slide-mounted material, as in Stiriinae, Cuculliinae, Heliiothinae, and basal plusiine tribe Omorphinini. The more derived Abrostolini display two subdorsal lobes directed medially. These fuse in Argyrogrammatini and Plusiini but leave a central rounded emargination. The ventral edge of the flange in Stictopterinae and Euteliinae is straight, with a median dorsal triangular inflection of T2 itself.

In general, the form of the T2 flange is highly invariant in large



FIGS. 12–16. *Ocalaria* antennae. 12, *O. quadriocellata* male; 13, *O. oculata* female; 14, *O. cohabita* male, lateral view; 15, *O. oculata* male; 16, *O. cohabita* female, lateral view. Scale line = 1 mm.



FIGS. 17-19. Male tergite 8. 17, *O. cohabita*; 18, *O. oculata*; 19, *O. quadriocellata*. Posterior edge uppermost, with transverse line marking posterior margin of abdominal segment 8. Scale line = 1 mm.

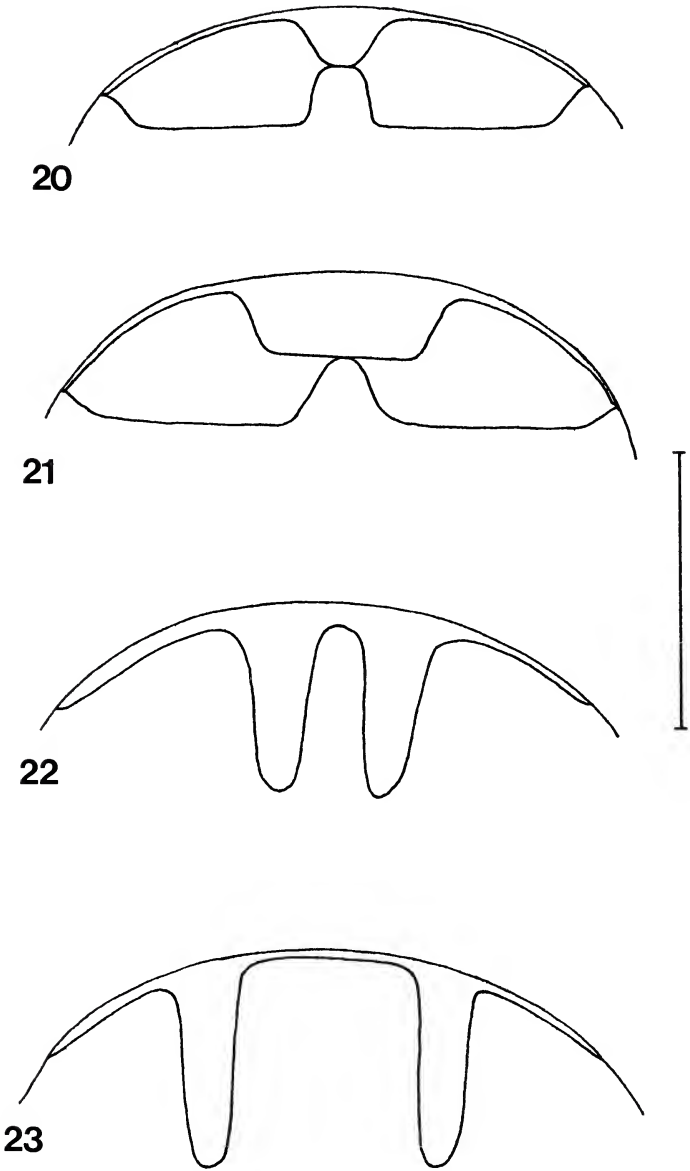
taxonomic groups, such as tribes or subfamilies. However, in *Ocalaria*, the T2 flange is remarkably variable between species. The putatively basal *O. cohabita* shows a sclerotized dorsal inflection of T2 similar to that in Stictopterinae and Euteliinae, but with the median emargination typical of "higher" plusiines. In addition, the ventral edge of the flange is somewhat cut back laterally. This flange is sexually dimorphic in *O. cohabita*, a feature almost certainly correlated with the dimorphism observed in sternite 2 (St2). The female (Fig. 21) differs from the male (Fig. 20) in that the median emargination is not parallel-sided, while the dorsal inflection is much broader and has a straight ventral edge.

*Ocalaria oculata* and *O. quadriocellata* differ markedly in lacking the sclerotized dorsal inflection and in the extreme specialization of the flange. *Ocalaria quadriocellata* has a T2 flange formed of two broad, ventrally-directed, well-separated rounded lobes (Fig. 22). This trend is more noticeable in *O. oculata*, in which the lobes are long, narrow, and closer to the lateral edges of T2 than to the center (Fig. 23).

St2 in *O. oculata* and *O. quadriocellata* is typically noctuid in form, with no marked diagnostic features. It is a roughly square sclerite (Fig. 25), with convex lateral and posterior edges. The anterolateral corners are produced into a pair of apodemes, from which a sclerotized bar arises laterally. This passes anteriorly to the counter-tympanal hood. The anterior margin of St2 is broadly U-shaped.

Females of *O. cohabita* have a broadly similar St2, but it is slightly squarer, with marginally concave lateral edges, and the anterior margin is more V-shaped (Fig. 24). St2 of male *O. cohabita*, however, is markedly different (Fig. 26), which may be the first record of sexual dimorphism in this structure in quadrifine noctuids. The whole sclerite





FIGS. 20–23. Tergite 2 flange. **20**, *O. cohabita* male; **21**, *O. cohabita* female; **22**, *O. quadriocellata* male; **23**, *O. oculata* male. Scale line = 1 mm.

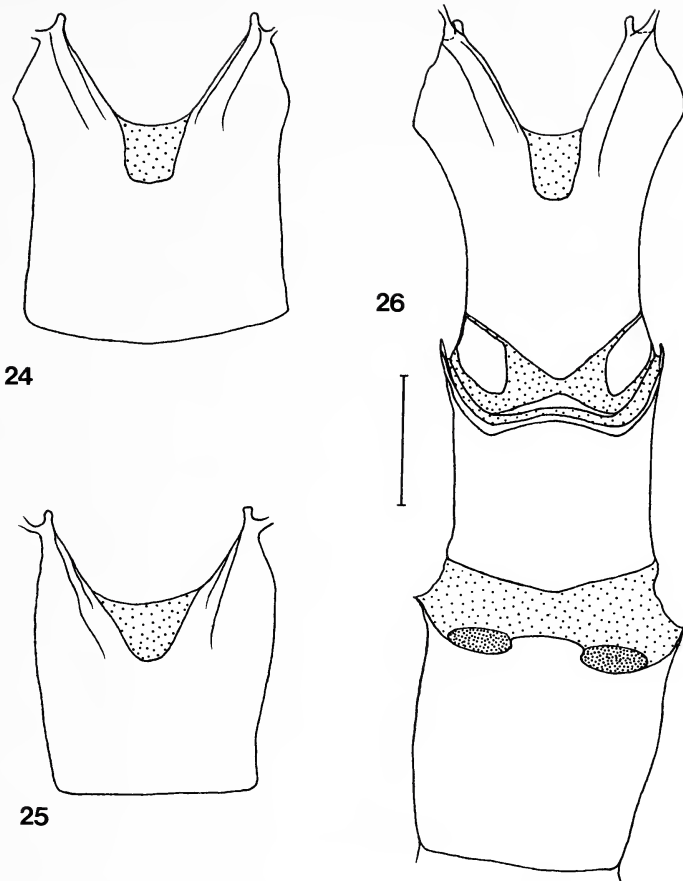
is elongate, with distinctly concave lateral margins. The anterior edge is V-shaped, while the posterior margin is produced as a broad, triangular point. Posterolaterally are two secondary sclerites in the inter-segmental membrane between St2 and St3. In addition, the anterior corners of St3 (Fig. 26) are produced around the posterolateral edges of these secondary sclerites, a feature similar to that seen in numerous trifine species, where it is associated with the lever of male basal abdominal hair pencils (Birch 1970). The posterior margin of St3 is also produced to a median point, but is more obtuse than that of St2. Finally, on the anterior edge of St4 (Fig. 26) are two concavities that appear to house shallow glandular pockets. The function of this complex in male *O. cohabita* is a matter for conjecture but suggests that adult biology, particularly courtship, of this species might be usefully studied.

**Male abdominal segment 8.** The form of the male eighth tergite (T8) and sternite (St8) displays species-level diagnostic features in a number of noctuid subfamilies; for example, Plusiinae (Dufay 1970), Stiriinae (Hogue 1963), Heliiothinae (M. J. Matthews pers. comm.). In addition, these sclerites have yielded characters useful in recognizing suprageneric taxa in Plusiinae (Kitching 1987).

The form of T8 in *Ocalaria* is characteristic, consisting of a median sclerotized longitudinal bar tapered posteriorly and expanded anteriorly. The three species differ in minor details: in *O. cohabita*, the bar does not reach the posterior margin of the segment and the anterior expansion has concave margins and a truncate apex (Fig. 17); in *O. oculata*, the anterior expansion is drawn out laterally into narrow points (Fig. 18); while in *O. quadriocellata*, the anterior expansion has a rounded apex (Fig. 19). In all three taxa, there appear to be two shallow pockets associated with the lateral edges of T8 anteriorly.

A8 bears a median weak tuft of hairs, barely differentiated into a pair of hair pencils, arising from a shallow, membranous, ventral pocket. St8 forms a thin sclerotized bar anterior to this pocket, with two concave bars running longitudinally on either side of the hair tuft. The anterolateral corners of St8 are produced as blunt triangular lobes. The form of St8 is similar in all three species, but whereas the anterior bar forms a blunt median point in *O. oculata* and *O. quadriocellata* (Fig. 11), in *O. cohabita*, it is broadly rounded with a somewhat straight central section (Fig. 10).

**Male genitalia.** *Ocalaria oculata* is very similar to *O. cohabita* (Fig. 3) except that the valve is of more uniform width basally, the saccus is acutely pointed and the aedeagal process is absent. In addition, the spines on the vesica basally are larger and more strongly sclerotized. Genitalia of *O. quadriocellata* are similar to *O. oculata* but the sacculus



FIGS. 24-26. *Ocalaria* sternites. 24, 25. Sternite 2. 24, *O. cohabita* female; 25, *O. quadriocellata* male; 26, Sternites 2-4 *O. cohabita* male. Scale line = 1 mm.

bears a small rounded lobe basally and the saccus forms a less acute point.

**Female genitalia.** The posterior margin of St8 bears a fringe of persistent, brown, setose scales that may be apomorphic for *Ocalaria*. *Ocalaria oculata* is essentially similar to *O. cohabita* (Fig. 4) but differs in that the corpus bursae is not differentiated from the ductus bursae, being merely a long, slightly broader membranous sac; the ductus bursae is broader with a median annulus of longitudinal ridges and sclerotized granulations; and the ostium bursae is adorned with sclerotized granulations. The anal papillae are diagonally cut back dorsally to the origin of the posterior apodemes. *Ocalaria quadriocellata* is broadly similar

to *O. cohabita*, except that the dorsoposterior parts of the anal papillae are drawn out into blunt, slightly downcurved points.

#### ACKNOWLEDGMENTS

This study was carried out partly during the tenure of a Junior Research Fellowship awarded by the Trustees of the British Museum (Natural History), which is gratefully acknowledged. I thank my colleagues at BMNH for support and comments, and the staff of the BMNH Photographic Unit for the photographs. Special thanks go to Nancy Greig and Philip DeVries for the opportunity to describe this species.

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#### ADDITIONAL MANUSCRIPT REVIEWERS, 1987

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## A NEW *SESIA* CLEARWING MOTH FROM MICHIGAN (SESIIDAE)

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**ABSTRACT.** *Sesia spartani*, new species was discovered in Michigan (30 males) in traps baited with a sex attractant consisting of 50:50 mixture of (3,13) Z,Z-ODDOH/(3,13) E,Z-ODDOH. The new species is described, illustrated, and compared with *S. tibialis* (Harris). The two differ in structure of male antennae, genital morphology, response to sex attractants, and seasonal occurrence.

**Additional key words:** *Sesia spartani*, *S. tibialis*, attractants.

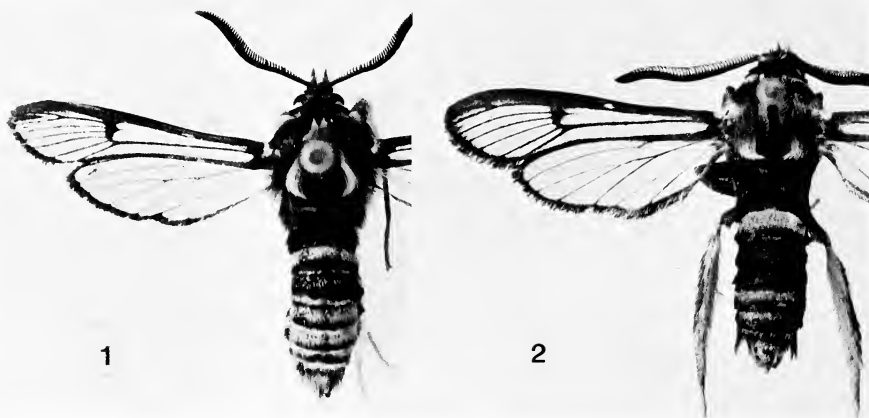
Use of synthetic sex attractants has resulted in the discovery of several new species of sesiids in the Western Hemisphere (Duckworth & Eichlin 1977a, 1977b, Greenfield & Karandinos 1979, Brown et al. 1985, Eichlin 1986, 1987).

During studies employing sex attractant baits to survey the Sesiidae of Michigan, a new species closely related to *Sesia tibialis* (Harris) was discovered and is described below. Males of *S. tibialis* (Fig. 2) are known to be very responsive to the Z,Z isomer of 3,13-octadecadien-1-ol acetate (Z,Z-ODDA) (Duckworth & Eichlin 1978:28), a major component of many clearwing moth pheromone systems (elucidated by Tumlinson et al. 1974). In Saskatchewan, Underhill et al. (1978) found the best attractant was probably a 80:20 blend of Z,Z-ODDA/Z,Z-ODDOH. The new species was discovered in the Lower Peninsula of Michigan when males were captured in traps baited with sex attractants consisting of a 50:50 mixture of the Z,Z and E,Z alcohols (Z,Z-ODDOH/E,Z-ODDOH). Traps baited with other sex attractants including that known to be effective for *S. tibialis* were deployed in the same areas throughout the collecting season but failed to capture any *S. spartani*.

### *Sesia* Fabricius

Genus *Sesia* is characterized by the following: Head with haustellum reduced, about  $\frac{2}{3}$  length of labial palpus; antenna strongly clavate, ventrally ciliate-unipectinate on male; horizontal flat plate of scales projecting somewhat over middle of eye. Forewing vein  $R_4$  terminating at apex,  $R_5$  below. Hindwing veins  $M_3$  and  $Cu_1$  joined at corner of cell or very short-stalked. Genitalia unique, generally as shown in Figs. 5 and 6.





FIGS. 1, 2. Adult males of *Sesia* spp. 1, *S. spartani*, Shiawassee Co., Michigan (holotype); 2, *S. tibialis*, Isabella Co., Michigan.

### *Sesia spartani*, new species

**Male** (Fig. 1). Head with vertex brown-black, some white posteriorly; front brown-black; occipital fringe white dorsally, yellow laterally; labial palpus roughened with long hairlike scales ventrally on basal segment, yellow with brown toward base; haustellum short, less than  $\frac{1}{2}$  length of labial palpus; antenna brown-black with yellow-orange at tip, unipectinate, individual middle segments with ramus about 3 times as long as the distance between 2 adjacent rami (dorsoapical view of antenna), produced from dorsoapical portion of segment (Fig. 3). Thorax brown-black with yellow behind collar, around wing bases, subdorsally on posterior half of mesothorax, and variously on metathorax. Abdomen brown-black but with broad yellow bands on segments 5, 6, and 7, less so on 4 dorsally; tip of abdomen mostly yellow with anal tuft poorly defined. Wings hyaline; narrow margins and discal spot brown. Wing length 8–9 mm (30 n). Legs with coxae brown-black edged with yellow; femora yellow dorsally, brown-black ventrally; tibiae yellow, hind tibia roughened dorsally by semierect, thin, elongate scales; tarsi yellow-orange. Genitalia as in Fig. 6.

**Female.** Unknown.

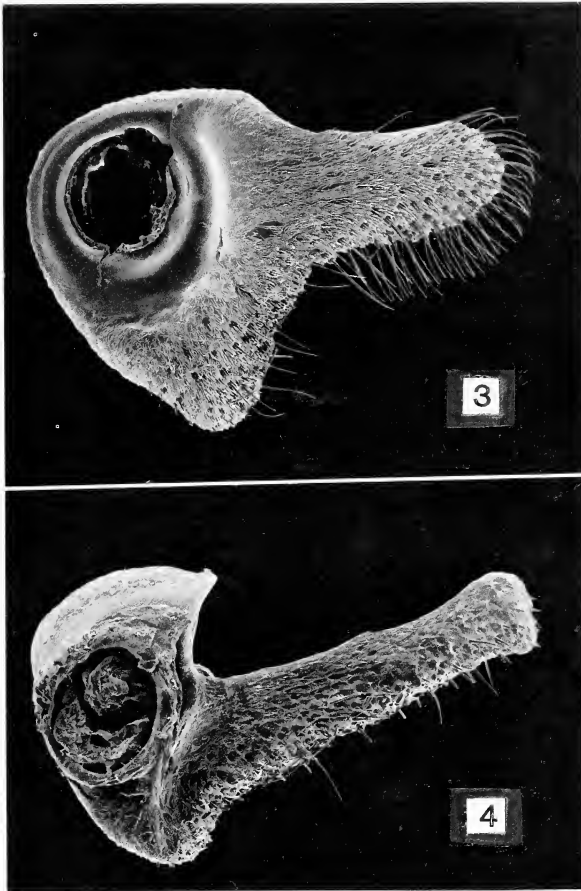
**Host.** Probably species of Salicaceae, particularly *Populus tremuloides* Micheaux (quaking aspen), based on observed larval damage to trees at the type locality and at other sites where *S. spartani* was collected.

**Distribution.** *Sesia spartani* has been collected in the Lower Peninsula of Michigan in Clinton, Shiawassee, and Lake counties.

**Types.** Holotype: Male, MICHIGAN: Shiawassee Co., Bath, 13 June 1987, Coll. William H. Taft; Rose Lake Wildlife Research Area, T5N R1E Sec 20; ZZOH/EZOH, 50:50; deposited in Entomology Museum, Michigan State University, East Lansing (MSU). Paratypes (29 males): 6, Shiawassee Co.: V-29-1987 (1); VI-9-1987 (2); T5N R1E Sec 20, 13 June 1987 (2); same as last except 14 June 1987 (1). 22, Clinton Co.: T5N R2W Sec 31, 13 June 1987 (3); same as last except 14 June 1987 (2); 16 June 1987 (4); 17 June 1987 (7); 19 June 1987 (2); 20 June 1987 (4). 1, Lake Co.: T17N R14W Sec 12, 14 June 1987 (all collected by William H. Taft using traps baited with ZZOH/EZOH 50:50).

Paratypes are deposited in MSU; U.S. National Museum of Natural History, Washington, D.C.; California Department of Food and Agriculture, Sacramento; Canadian National Collection, Ottawa, Ontario; and Field Museum, Chicago, Illinois.

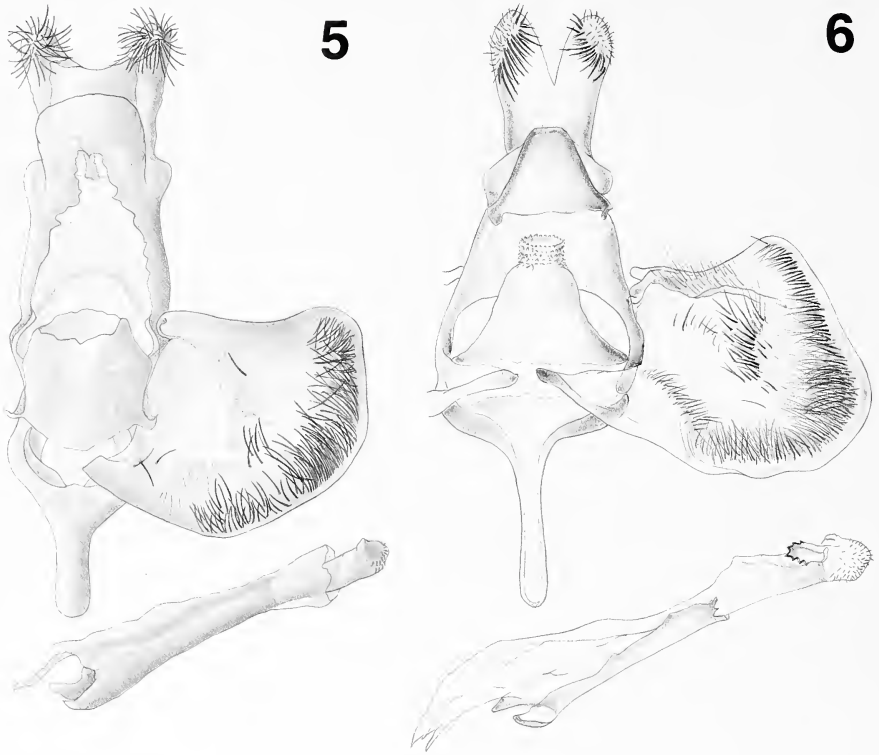
**Discussion.** *Sesia spartani* is superficially similar to *S. tibialis*. However, male genitalia



FIGS. 3, 4. Segments from near middle of left antennae of *Sesia* spp. as viewed ventrally on proximal surface by scanning electron microscope. **3**, *S. spartani*; **4**, *S. tibialis*.

differ considerably (Figs. 5, 6): *S. spartani* uncus deeply and acutely divided, cleft of *S. tibialis* uncus less deep, broadly rounded; saccus about  $\frac{1}{2}$  length of valve, only  $\frac{1}{3}$  on *S. tibialis*; valve more produced ventroposteriorly and with more thick, dark spines near center than on *S. tibialis*; gnathos narrowing apically and of different form than for *S. tibialis*; and aedeagus with jagged plate posteriorly, *S. tibialis* lacking jagged plate. Some specimens of *S. tibialis* from Michigan (Fig. 2) are nearly lacking yellow dorsally on abdominal segments 4 and 5, while on *S. spartani* segment 5 is mostly yellow, and 4 has some yellow powdering. *Sesia tibialis* from elsewhere usually has yellow banding on all segments.

The collecting sites were low muck soil depressions in scattered locations. These habitats are characterized by large stands of regrowth quaking aspen mixed with willows (*Salix* spp.), elm (*Ulmus* sp.), red maple (*Acer rubrum* L.), and black cherry (*Prunus serotina* Ehrh.). The undergrowth is dogwood (*Cornus* sp.), viburnum (*Viburnum* sp.), and blueberries (*Vaccinium* sp.).



FIGS. 5, 6. Male genitalia of *Sesia* spp. viewed ventrally, left valve removed. 5, *S. tibialis* (from Duckworth & Eichlin 1978); 6, *S. spartani*.

The *S. spartani* males were captured in Multi-pher #1® plastic pheromone traps. Collecting dates for *S. spartani* were 29 May–20 June 1987. *Paranthrene dollii* (Neumoegen) was collected with *S. spartani* during late May and early June. At the time of capture, the growing season was 250–300 degree-days (base 50) above normal; consequently, in normal years *S. spartani* may fly later in June or in early July. It appears to fly two weeks to a month earlier than does *S. tibialis* in Michigan. *Sesia tibialis* has not been found in counties where *S. spartani* originated, but has been collected as far south as Newaygo, Isabella, and Midland counties, and is known from Nova Scotia and New England to British Columbia, and from the Rocky Mountains to the Pacific Coast. The Michigan habitats for both species appear to be similar.

This species is named for the Spartans, a nickname applied to Michigan State University athletic teams.

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## TWO NEW SPECIES OF *RHYACIONIA* PINE MOTHS FROM MEXICO (TORTRICIDAE: OLETHREUTINAE)

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**ABSTRACT.** *Rhyacionia cibriani* is described from five males and five females, and *R. rubigifasciola* from one male and one female. The former is differentiated from *R. jenningsi* Powell by genital and other characters including longer antennal pecten. The latter is differentiated from all congeners, none of which it resembles closely, by genital characters including a ridge separating sacculus and valval neck in the male, and an anally emarginate sterigma in the female. *Pinus hartwegii* Lindl. and *P. oocarpa* Schiede are the respective hosts, the larvae boring in branchlets. The new species bring the number of *Rhyacionia* known in Mexico and the Neotropics to nine species.

**Additional key words:** taxonomy, Eucosmini, *Rhyacionia cibriani*, *R. rubigifasciola*, Neotropics.

Pines, the larval hosts of *Rhyacionia*, are numerous in Mexico, 21 of the 30 pine species occurring there being absent in the U.S. (Critchfield & Little 1966). The 2 new species described here bring the number of *Rhyacionia* known in Mexico and the Neotropics to 9 species (Powell & Razowski in press), and the number described worldwide to 34 (Miller 1985, Obraztsov 1964, Powell & Miller 1978). This is the fourth paper in a series in which I describe new Neotropical olethreutines in various genera whose hosts and modes of feeding make them of economic interest or importance (Miller 1966, 1986, 1987).

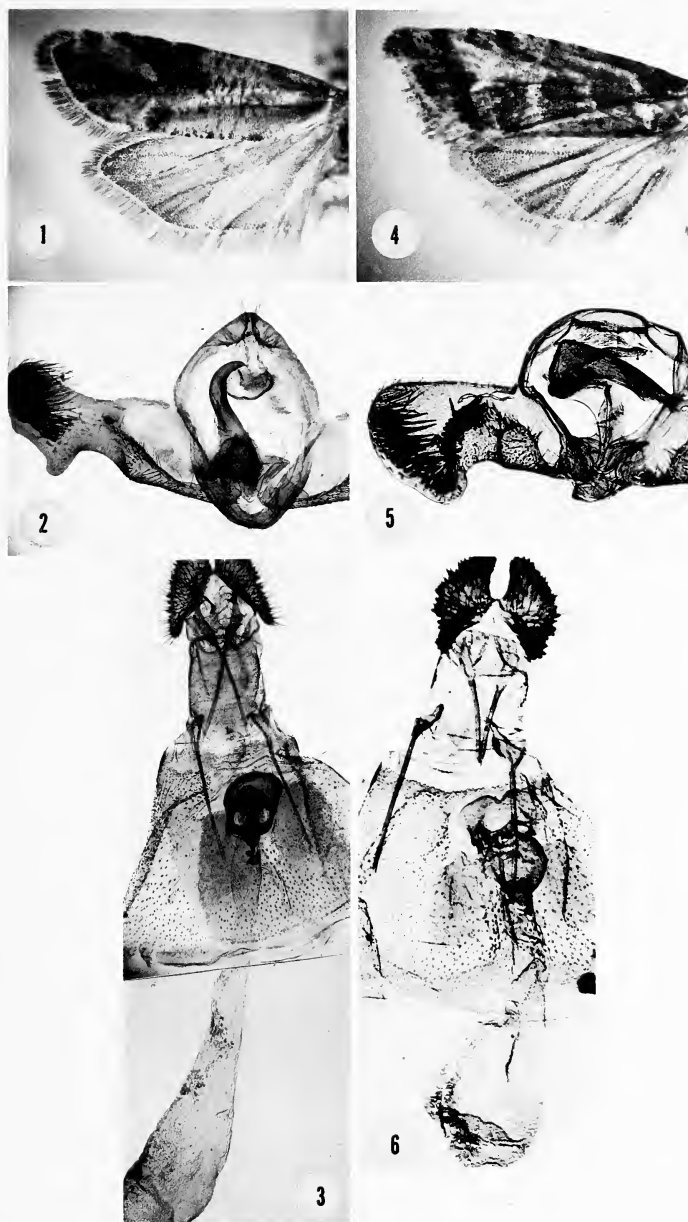
In both species described here, hindwing vein  $M_2$  is bent at its base, and hindwing veins  $M_3$  and CuA are either stalked or connate and approximate toward their bases. These character states place the species in Eucosmini (Obraztsov 1958). Features that place them in *Rhyacionia* are italicized in descriptions. Venation was ascertained under a stereomicroscope from temporary preparations made by touching xylol to wings while light passed through them (Zimmerman 1978).

### *Rhyacionia cibriani*, new species

(Figs. 1-3)

**Male.** Forewing length 11.0 to 12.0 mm (holotype 11.0 mm) (5n). **Head.** Labial palpus clothed with brown-banded white scales, length of 2nd segment  $2\times$  eye diam., length of 3rd segment  $\frac{1}{2}$  that of 2nd; vestiture of vertex similar to that of labial palpus; antennal pecten length 1 to  $1\frac{1}{4}\times$  flagellar length,  $1\frac{3}{4}$  to  $2\times$  flagellar diam. **Thorax.** Dorsal vestiture beige, ventral paler; front and middle leg scaling similar to that of labial palpus, hind leg paler, tarsi indistinctly white-banded; *forewing with veins  $M_2$  and  $M_3$  connate, termen straight or convex, costal fold absent*, upper side yellowish to coppery red, tinged with lavender in cell area, crossed by irregular striae near middle (Fig. 1), underside pale grayish yellow; hindwing upper side gray, underside paler than forewing underside. **Genitalia** (Fig. 2) (3n). *Valva lacking costal hook*, a ridge from sacculus to neck terminating in a nipplelike process at mid-neck, neck constricted to nearly  $\frac{1}{2}$  maximum sacculus





FIGS. 1-6. 1-3. *Rhyacionia cibriani* from type locality. 1, Wings of paratype; 2, Male genitalia of holotype; 3, Female genitalia of paratype. 4-6. *R. rubigifasciola* from type locality. 4, Wings of holotype; 5, Male genitalia of holotype; 6, Female genitalia of paratype. Additional information keyed to figure numbers appears in Type Data section. Some negatives reversed.

width, *pollex present* and its length about  $\frac{1}{4}$  maximum cucullus width; *uncus and socii rudimentary or absent*; aedeagus curved and tapering toward apex, vesica with 3 to 4 cornuti.

**Female.** Forewing length 9.5 to 11.0 mm (5n). Similar exteriorly to male except for shorter antennal pecten. **Genitalia** (Fig. 3) (3n). Sternum 7 emarginate; sterigma nearly square in outline, laterally inflected, with a broad and evenly rounded longitudinal ridge; ductus bursae sclerotized only near ostium bursae; corpus bursae with 1 thornlike signum, sometimes a tiny 2nd one.

**Type data.** Holotype male, Paso de Cortez, Méx., Mexico, 12 March 1984, No. 1133, *Pinus hartwegii* Lindl., D. Cibrián, genit. prep. WEM 1910844 (Fig. 2), in U.S. National Museum of Natural History, Washington, D.C. Four paratype males, same data as holotype except 5–9 April 1984, 2 genit. preps. WEM 910842 and WEM 84885; 5 paratype females, same data as holotype except 5–16 April 1984 (Fig. 1), 3 genit. preps. WEM 910843 (Fig. 3), WEM 2210841, and WEM 53882, in U.S. National Museum of Natural History; Essig Museum, University of California, Berkeley; University of Minnesota, St. Paul; and Lab. de Entomologia Forestal, Universidad Autónoma Chapingo, Chapingo, Mexico.

**Discussion.** *Rhyacionia cibriani* most resembles *R. jenningsi* Powell, but differs in size, structure, and forewing pattern as follows. *Rhyacionia cibriani* has a 40% greater average forewing length, 100% greater relative length of 2nd palpus segment, and 350 to 400% longer relative antennal pecten length than *R. jenningsi*; the lavender hue of the *R. cibriani* forewing cell is lacking in *R. jenningsi*; the nipplelike process on the male valva in *R. cibriani* is lacking in *R. jenningsi*; the 7th female sternum is more deeply emarginate in *R. cibriani* and the sterigma more square than in *R. jenningsi*. The foregoing character states for *R. jenningsi* are documented in Powell and Miller (1978).

*Pinus hartwegii* is classified in *Ponderosae* (Critchfield & Little 1966), a *Pinus* subsection whose members are hosts to several *Rhyacionia* species (Powell & Miller 1978).

The species is named for David Cibrián-Tovar, who reared adults from larvae boring in *Pinus hartwegii* branchlets.

### *Rhyacionia rubigifasciola*, new species

(Figs. 4–6)

**Male.** Forewing length 8.5 mm (1n). **Head.** Labial palpus clothed with silvery white scales sometimes tinged with orange or gray, length of 2nd segment  $1\frac{1}{2} \times$  eye diam., length of 3rd segment  $\frac{1}{4}$  that of 2nd; vestiture of vertex silvery white except for orange near antennal bases; antennal pecten length  $0.8 \times$  flagellar length,  $0.8 \times$  flagellar diam. **Thorax.** Dorsal vestiture similar to vertex; front and middle legs orange, banded with white, hind leg paler except for tarsi; *forewing with veins  $M_2$  and  $M_3$  connate, termen convex, costal fold absent*, upper side with 4 orange spindle-shaped fasciae extending from costa to dorsum, 2 less tapered ones from costa to termen, all separated by silvery white (Fig. 4), underside pale gray; hindwing upper side gray, underside paler than forewing underside. **Genitalia** (Fig. 5) (1n). *Valva lacking costal hook*, sacculus separated from neck by a ridge, neck scarcely constricted dorsoventrally, concave anally, *pollex present* but not well defined in outline; *uncus absent*; *socii tiny, inflected, nearly obscured by tergum*, aedeagus apically expanded, forked, with several tiny apical spurs; vesica with 6 cornuti.

**Female.** Forewing length 8.5 mm (1n). Similar exteriorly to male. **Genitalia** (Fig. 6) (1n). Sternum 7 not markedly emarginate; sterigma rounded in outline, emarginate on anal margin, lamella antevaginalis scoop-shaped; ductus bursae sclerotized in an incomplete ring for a short distance at  $\frac{2}{3}$  its length from ostium bursae; corpus bursae with 2 thornlike signa.

**Type data.** Holotype male, Sta. Lucia, Sinaloa, Mexico, 1 July 1981 (Fig. 4), No. 802, *Pinus oocarpa* Schiede, D. Cibrián & T. Méndez, genit. prep. WEM 108842 (Fig. 5), in Essig Museum, University of California, Berkeley. One paratype female, same data and depository as holotype except genit. prep. WEM 234851 (Fig. 6).

**Discussion.** *Rhyacionia rubigifasciola* does not clearly resemble any congener (Miller 1985, Obratsov 1964, Powell & Miller 1978). It differs from all in male valval outline

and in the ridge separating sacculus and neck; also in shape of the female sterigma with its anal emargination. The larvae bore in *Pinus oocarpa* branchlets.

*Pinus oocarpa* is classified in *Oocarpae* (Critchfield & Little 1966), a *Pinus* subsection whose members are hosts to only one other *Rhyacionia* species, *R. pasadenana* (Kearfott) (Powell & Miller 1978). The new species does not appear closer morphologically to *R. pasadenana* than to other *Rhyacionia* species, however.

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## BOOK REVIEWS

THE BUTTERFLIES OF COSTA RICA AND THEIR NATURAL HISTORY: PAPILIONIDAE, PIERIDAE, NYMPHALIDAE, by Philip J. DeVries (illus. by P. J. DeVries, Jennifer Clark and R. Cubero). 1987. Princeton Univ. Press. xxii + 327 pp. Hardback, ISBN 0-691-08420-3, \$60.00; paperback, ISBN 0-691-02403-0, \$22.50.

Costa Rica is an exceptionally delightful Central American country with a happy and friendly people (they abolished their military some years ago and used the money recovered for education), gorgeous landscape, and a surprisingly complete complement of beautiful Neotropical butterflies which are ably described, discussed, and made known in intimate detail in this book.

For the three families covered, this is a *very* good book on Neotropical Lepidoptera, and will be most useful (especially at the low price for the paperback edition) to anyone interested in these families from central México southwards. It could be a better book still; it contains a rather high density of errors of nomenclature, fact, writing, and interpretation which should be corrected in the second edition (which surely will be necessary as several thousand copies have already been sold). A list of these has been given to the author; only some more important facets can be commented on here, probably most usefully to those who have already bought the book. If you haven't, you should as soon as you plan to work on the Neotropical fauna in the three families.

DeVries has lived for almost 10 years in Costa Rica, working at the National Museum of Natural History with top Costa Rican scientists, and maintaining ties with many foreign scientists studying natural history in this Country (mostly through the Organization for Tropical Studies; a general volume entitled *Costa Rican Natural History*, edited by Daniel Janzen, recently appeared, and covers many aspects of this work), and also in other Central American countries (especially the Muysshondts, active in El Salvador). He is responsible for the discovery of many species in Costa Rica, verification of their habitats and foodplants, and description of their early stages, and is surely well qualified to produce this book. The text was written mostly during periods in Austin, Texas, and the British Museum; the color plates, of high quality but reduced a little too much for optimal usefulness, were prepared in the latter institution, at times using non-Costa-Rican or older specimens, with faded colors or tattered wings.

Strong points of the book include maps of the Country with roads, cities, topography, and parks (but with a wrong scale; 50 km on the scale given are actually 82 km on the map), a refreshing emphasis on natural history and juvenile biology with much valuable new data, a useful list of butterfly-enemy groups (p. 18), a sensible and eclectic position on systematics (p. 32), a recommendation for taking notes rather than specimens in the field (p. 33) and use of binoculars and simple camera equipment to increase the value and number of observations (p. 37), a good grasp of the Costa Rican faunal regions showing much first-hand experience (though perhaps not enough yet in cloud-infested Atlantic coastal forests), recognition of certain behavioral traits such as "only new males visit wet sand", an excellent job of correlating illustrations with types in difficult groups like *Memphis*, *Adelpha*, *Phyciodes* (s.l.), and *Euptychiini* which will be useful to many (if all are correct), and palatability data on many species. Line drawings of juveniles are strikingly clear and correct.

DeVries' youthful enthusiasm, which made this book possible and contributed greatly to its notable authority, style, grace, and the breadth and interest of its natural history accounts, gets the best of him in diverse parts of the book. His statement in the Preface that, when he began to work in Costa Rica in the 1970's, "nobody was willing to do a detailed study of the Neotropical butterfly fauna" is bound to earn some grumbles from the many "nobodies" who have willingly and tirelessly labored in this task since Müller (1870's) and Moss (1900's) started doing broad work on natural history of Brazilian Lepidoptera; several dozen are now active, many in fact quoted in the large Bibliography (382 references). An unexpected unfamiliarity with recent work in Mexico, such as that on *Parides* (mostly published in the *Rev. Soc. Mex. Lepid.* mentioned on p. 53 but cited only 3 times in the Bibliography), and in South America since Müller and Moss, sometimes

leads to unnecessary affirmations or contradictions; in species ranges, 10 genera and 58 species common in southeastern Brazil are indicated as reaching only the Amazon Basin, 10 others have their southern limits shrunk appreciably (sometimes all the way to Central America) and many groups are indicated as "reaching their maximum diversity in the Amazon Basin" when in fact this occurs on the lower Andean slopes (as indicated correctly in *Prepona*)—Amazonian to be sure but only a small, special part of the Basin, over almost all of which butterfly diversity is quite low. Peterson's classic 1948 work on larvae is not mentioned (p. 6), and the list of parasites omits mites (p. 17). The affirmation that "the effects of parasitoids on populations of tropical butterflies are unstudied" (p. 17) makes one wonder what the author accepts as a study (there are dozens of purported scientific papers published in this area). Likewise, the generalization that "toxins in adult butterflies are probably entirely directed at vertebrate predators" (p. 23) is indefensible. That Neotropical diversity "remains one of the great challenges in evolutionary biology" (p. 57) again ignores much serious work done recently by many Neotropical and other scientists. In a perhaps Freudian slip, several medicinal (official) plant species are spelled "officionale", and misspelled plant families (new synonyms?) include Vochysiaceae ("Vouchysiaceae", p. 66, 68), Canellaceae ("Cannelaceae", p. 61), Quiinaceae ("Quiiniaceae", p. 109, but correct on p. 112), and Verbenaceae ("Verbenaeeaceae", p. 76). Ithomiinae venations on p. 215 are so poorly drawn that they will confuse, not help the reader. The late Walter Forster would surely be disappointed at DeVries' summary dismissal of almost all his Euptychiine genera, many of which are sound natural groupings. Nomenclatural corrections and changes necessary (\*) or suggested include at least the following (which should be noted also on the check-list, pp. 291 ff):

Page	Name given	Should be	Comments
18	*Tyrannidae	Tyrannidae	—
41	* <i>Hamadryas iphthime</i>	<i>H. iphthime</i>	—
65	* <i>Parides alopius</i>	(delete)	Nicaraguan record an error.
	* <i>P. dares</i>	(delete)	A unique hybrid ( <i>photinus</i> × <i>montezuma</i> ).
67	* <i>P. arcas</i>	<i>P. eurimedes</i>	<i>Arcas</i> a homonym.
69	* <i>Battus belus varus</i>	<i>B. latinus</i>	<i>B. varus</i> is Amazonian, female <i>latinus</i> monomorphic throughout range.
70	<i>B. crassus</i>	<i>B. crassus lepidus</i>	Transandean subspecies.
75	<i>Papilio victorinus</i> , <i>P. cleotas</i>	(probably one species)	Would be useful to hybridize these in Costa Rica.
77	<i>Eurytides ilus</i> , <i>E. brachus</i>	(probably one species)	—
78	* <i>E. protesilaus dariensis</i>	(includes <i>E. macrostlaus</i> )	Should separate.
89	* <i>Archonias eurytele</i>	<i>Charonias eurytele</i>	Well differentiated genera; also Fig. 7.
97	* <i>Perrhybris pyrrha</i>	<i>P. pamelae</i>	<i>Pyrrha</i> a homonym; also Fig. 7.
99	<i>Ascia limona</i>	<i>A. buniae limona</i>	Probably conspecific.
113	* <i>Prepona omphale</i>	(includes <i>P. laertes</i> )	Should separate.
115	* <i>P. meander amphimachus</i>	(two different species)	Separate.
116	<i>Zaretis ellops</i> , <i>Z. itys</i>	(probably one species)	Widespread polymorphism all over Neotropics; seasonal.
144, 145	<i>Dynamine hecuba</i> , <i>D. sosthenes</i>	(probably subspecies of South American species)	—



	<i>D. glauce</i>	<i>D. artemisia glauce</i>	—
142	* <i>Myscelia orisis</i>	<i>M. orsis</i>	—
153	<i>Eunica venusia</i> , <i>E. augusta</i>	<i>E. volumna venusia</i> , <i>E. caelina augusta</i>	—
154	* <i>Cantonephele</i>	<i>Catonephele</i>	—
161	* <i>Haematera pyramus</i>	<i>Callidula pyrame</i>	Senior synonym, same species.
162	* <i>Pseudonica</i>	<i>Nica</i>	Senior synonym, <i>Nica</i> used on p. 156.
163	<i>Diaethria marchallii</i>	<i>D. clymena marchallii</i>	—
182	* <i>Turnera ulmnifolia</i>	<i>T. ulmifolia</i>	—
183	* <i>Actinote leucomelas</i>	<i>Altinote ozomene nox</i>	Well separated genus, older name.
185	* <i>A. melampeplos</i> , <i>A. guatemalensis</i>	<i>A. pellenaea</i> subspecies (both)	—
186	* <i>Heliconius sappho</i>	<i>H. sappho</i>	—
188	<i>Dione juno</i>	<i>D. juno huascuma</i>	Central American subspecies.
191	* <i>Eueides lybia lybioides</i> (first mention, (Fabr.))	<i>E. lybia olympia</i>	—
193	<i>Heliconius doris</i>	<i>Laparus doris</i>	Well differentiated genus.
192	* <i>Eueides isabella zoracon</i>	<i>E. isabella zorcaon</i>	—
207	* <i>Napeogenes peredia</i>	<i>N. peridia</i>	See also p. 46, fig. 7.
221	* <i>Callithomia hexia</i>	<i>C. hezia</i>	—
224	* <i>Ithomia diasia</i>	<i>I. diasia</i>	—
226	* <i>Prestonia portabellensis</i>	<i>P. portobellensis</i>	—
230	* <i>Godyris zavaleta sorites</i>	<i>G. zavaleta caesiopicta</i>	Senior synonym.
240	* <i>Hyaliris</i>	<i>Hyaliris</i>	Popular misspelling.
241	<i>Antirrhaea miltiades</i> , <i>A. tomasia</i>	(should be one species)	Reason for separation not convincing.
249	<i>Brassolis isthmia</i>	<i>B. sophorae isthmia</i>	Probably monotypic genus.
257ff	<i>Euptychiini</i> (esp. <i>Euptychia mollina</i> , <i>Cissia terrestris</i> )	(many Amazonian names pulled in incorrectly for Central American species. Nomenclature here a big step forward but still lacks refinement)	—
262	* <i>Callitaera</i> (for <i>polita</i> )	<i>Cithaerias</i>	Older synonym, correct on p. 260.
275	* <i>Cissia libye</i>	<i>C. libyoidea</i> (Butler) (or <i>Magneptychia</i> )	Transandean species has different chromosomes from Guianan type.
276	* <i>Cissia hesione</i>	<i>Pareuptychia ocirrhoe</i>	<i>Hesione</i> a homonym.

Plate errors include illustration of *Papilio paeon* as *P. cresphontes* (Plate 4; *P. paeon* not mentioned in text); inversion of names for *Danaus gilippus* and *D. eresimus* (Plate 33); and illustration of a probable *Caligo oileus* (indicated as "not illustrated" in text) as *C. illioneus* on Plate 46, no. 2. Figure 7 (a "tipped in" plate following p. 26) was missing from the paperback copy purchased for my University library.

A selection of additional irksome errors (unfortunately, there are many more, some quite misleading) includes the following. There is a general lack of detailed information on variation in juveniles (very frequent in my experience), accentuated by sketchy, often inscrutable or generalized, or even wrong (as in *Papilio*, *Hypothyris*) descriptions, and few mentions of the number of replicates of rearing (thereby many opportunities to help

in juvenile field identification lost). There occurs an implicit advocacy of collection in nature reserves (p. 33); recent work on endangered species in Brazil suggests that even limited collecting of adults or juveniles of rare or local species in some kinds of habitats can seriously depress subsequent generations. Species lists for the Carrillo Belt are repeated (pp. 47, 49). Many place names mentioned in text are missing from maps (but usually are present in the gazetteer, pp. 285–287, where only one locality—Rincon, Osa—was found misplaced, 160 km to the NW). Data on canopy faunas are anecdotal, and seem overemphasized, or else are much more important in Costa Rican topography than in the flatter Amazon Basin. Diversity comparisons (p. 52) use only two sites in each of the six regions; only near-asymptotic lists, which these are probably not, can give a reliable picture. A number of generalizations presented in family, tribe or generic accounts are not obeyed by many included taxa, such as “tailless and sexually dimorphic troidines” (not *Parides photinus* or *P. montezuma*) with “white woolly scent scales” (not *P. eurimedes*), and “mimetic Dismorphiines” (not the majority listed). Inference of larval host plant from pupal placement for *Papilio cleotas* (fide W. Haber) would permit *P. anchisiades* to eat my back door, over 30 m from the nearest *Citrus* they actually fed upon; some go much farther. The book’s author doubts that male *Battus* visit sand (normal all over South America), that male *Eutresis* visit pyrrolizidine alkaloid sources (frequent in Venezuela and Colombia), that pterin pigments occur outside Pieridae (present in most butterflies, at times in large quantities), or that mimetic charaxines occur outside *Consul* (he illustrates several without commenting on their mimicry). He mixes up the characters in describing seasonal forms of *Eurema proterpia* (p. 105, compare Plate 10), and uses an-idi ending for “subfamily or tribal status” (p. 127). He indicates 10 species in *Libytheana* (there are 3), 2 in *Baeotus* (there are 3), “a few” in *Eutresis* (probably only 2), 5 in *Brassolis* (probably all 1), 10 in *Cithaerias* (probably 3 or less), 1 in *Dulcedo* (few know about the 2nd high-elevation west Colombian species, *D. mimica*). He restricts *Nessaea* to swamp forests, though it occurs on mesic hillsides in many parts of South America. Female behavior of *Callidula pyrame* (“*Haematera*”) is generalized to both sexes. The red basal dots on the ventral hindwing of *Heliconius* are transferred to the forewing. *Microtia* is placed in the Melitaeini on p. 198, in the Phycioidini on p. 205. A dropped line on p. 213 grows wing-pads on *Lycorea* larvae. The interesting mimicry situations involving *Caligo atreus*-*Antirrhoea pterocarpa*-female *Catoblepia orgetorix* and *Drucina leodonta*-*Tithorea tarricina* need comment; the second is simply denied (it occurs in Panamanian Chiriqui), the first involves birds’ wariness at the large size and eyespots of *Caligo* who can even keep birds away from their feeders.

These diverse “gripes” could go on, but will tire the reader. They are not intended to subtract from the value of the book, but to add to that of future editions, avoiding a wide circulation of inconsistencies and misinformation. In relation to most current books covering parts of the Neotropical butterfly fauna, this one stands out in general as carefully written, taxonomically accurate, biologically important, ecologically interesting, and sane. This is, in part, a negative reflection on the others.

It seems interesting to compare this book with the only other well illustrated modern single-country butterfly guide for the Neotropics, Barcant’s 1970 *Butterflies of Trinidad and Tobago*. Prepared by an amateur and lifetime Trinidad resident, and aimed at nature lovers, children, and collectors, this book received such a negative and unfair review in this journal that its author remained deeply embittered until his death last year. It covered the complete lot of families (with rather inscrutable plates for Lycaenidae and an outdated list for Hesperidae); its color illustrations were generally of high quality and esthetic balance, showing recently captured specimens with no damage. Emphasis was likewise on natural history, though with less information on juveniles and foodplants, to the point of using an arrangement based on habitat rather than taxonomy; coverage of historical, traditional and folklore aspects was strong, with common names in Trinidad given for many species. Barcant was not familiar with modern ecological pattern and theory as is DeVries, which sometimes detracted and other times helped his book (many such aspects have notoriously short half-lives). Both books give many specific details on collecting localities, adult habitats, mimicry, seasonality, physical geography and general methods; Barcant is more “folksy” while DeVries is more “objective”.

It is to be hoped that DeVries' book reaches a wider readership today than did Barcant's 18 years ago, and will continue to stimulate and aid those who study the fullness of biological aspects of Neotropical butterflies, and who wish to publish such well illustrated regional accounts in the future. All of these, like the Barcant and DeVries books, should be of immeasurable assistance in biological and ecological studies in the Neotropics, as well as useful and enjoyable to amateurs.

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BUTTERFLIES OF NORTH DAKOTA: AN ATLAS AND GUIDE, by Ronald Alan Royer. 1988. Science Monograph No. 1, Division of Science, Minot State University, Minot, North Dakota 58701. Format 14 × 20 cm, 192 pp., 12 pp. color plates, 1 b/w plate, 30 pp. maps. Plastic spiral binding. Soft cover. \$14.95.

The author has brought together in a single volume a guide and atlas which describes with text, color plates, and distribution maps all 142 species of butterflies known to occur in North Dakota. The book succeeds in fulfilling the author's goal of providing access to the Lepidoptera literature for the state.

The book begins with an Introduction which includes an explanation of the binomial system, North Dakota environments, terminology (wing surface and venation), and scope and use of the book. This is followed by the Guide, which includes a narrative for each species. Each species is introduced with the common and binomial name (including full author name), and corresponding plate number. The Atlas includes a State map with counties named followed by a State map for each species with the counties of record spot marked. There are five maps on the left side of each page with space on the right for notes. Plates are 60% natural size photographs of actual specimens. Opposite each plate, the binomial name, sex, view (dorsal or ventral), collection locality, and date collected are arranged according to how specimens appear in the plate. Next is a Hypothetical and Erroneous Records List followed by a list of names and addresses of lepidopterist organizations and suppliers. The Bibliography follows, then a 121 word Glossary, and finally the Index of Butterflies listed by binominal and common names with page numbers for the Guide, Atlas, and Plate sections.

Some of the nice things about this volume have already been mentioned, but still others are obvious when you pick it up—the sturdy binding and quality paper are suited for years of use. The cover is dominated by a photograph of *Hesperia dacotae* (Skinner), a nice touch. Coverage is complete and you could not ask for more information in the species descriptions. The author follows the 1981 Miller & Brown generic naming system, and there are no taxonomic surprises.

The faults with the book are few considering the wealth of information presented. The map in the Introduction shows only the major life zones. A more detailed map should have named the major rivers, drainage systems, and geographical features. Repeating the named counties map would have been helpful, too. Reading this section makes one feel the book was written for North Dakota collectors already acquainted with the State rather than for collectors who find themselves in North Dakota. The terminology section would have benefited with an explanation of how to distinguish the sexes, and with a generalized diagram of external morphological characters. The chapter might also have included a brief discussion of butterfly evolution, clarifying the hierarchy used in the book. There are no keys except one to the Papilionoidea.

Most of my comments concern the Guide and Plates chapters. The desired information is there, but would have been easier to locate if headings such as Description, Similar

Species, Life Cycle, Flight, Habitat, and Range were inserted in bold type in the text. The text is not cross-indexed except for a Plate number with each species description. The Guide, Atlas, and Plates sections should have included page numbers for the corresponding sections which would have helped tie the chapters together. The color plates are of good quality, and my only change would have been to adjust background colors of Plates II and IV to increase contrast. Illustrated specimens should have been numbered, with those numbers repeated in the Plate legend. This would have helped Plate II, as the extreme example, where 56 specimens are pictured, and searching the legend for the binomial name is tedious. A simple checklist at the end would have been useful to some collectors, or perhaps a box to check by each distribution map.

The faults with the book are few, and my criticisms also apply to a number of other popular books and field guides. This book is a valuable source of information. Whether or not you are ever fortunate enough to collect in North Dakota, this handsome book is a must for the naturalist.

R. D. PETERSON II, *Biosciences Research Laboratory, ARS-USDA, P.O. Box 5674, Fargo, North Dakota 58105.*

*Journal of the Lepidopterists' Society*  
42(3), 1988, 245

THE MOTHS OF BORNEO: SUPERFAMILY BOMBYCOIDEA: FAMILIES LASIOCAMPIDAE, EUPTEROTIDAE, BOMBYCIDAE, BRAHMAEIDAE, SATURNIIDAE, SPHINGIDAE, by Jeremy D. Holloway. 1987. Southdene Sdn. Bhd., P.O. Box 10139, Kuala Lumpur 50704, Malaysia. 199 pages, 20 color plates. Paperback. About \$35.00.

This book deviates from other faunistic treatments by including more detail on phylogeny and ecology, particularly hostplants. The color plates were produced by Bernard D'Abrera, so are predictably of high quality. All known species in these families from Borneo are treated in the text and depicted in color, thus including a considerable portion of the Indo-Australian moth fauna. The text draws from observations and works published in Asia by resident entomologists, and manifests Holloway's own extensive field experience in the region; the result is far beyond what could be produced from study of museum specimens alone. Where new or controversial taxonomic decisions are enacted, the author faithfully provides justification or explanation.

Inclusion of Sphingidae within Bombycoidea is unexpected. Upon reading the discussion of characters to justify this, I was a little disappointed, but apparently seven synapomorphies do link sphingids to other bombycoids. Such a large superfamily, now comprising 13 or 14 families worldwide, makes it difficult to designate nomenclaturally the closer relationships within the group; one wishes for a category between superfamily and family levels (or between suborder and superfamily levels) to remedy the situation. Holloway's discussion of the phylogeny of those families makes the book useful to Lepidoptera taxonomists around the world, even to those who profess no interest in moths of south-eastern Asia. The book is well done. I found no typographical errors. I believe those who acquire it will wish to purchase other volumes in the series, most of which are as yet unpublished.

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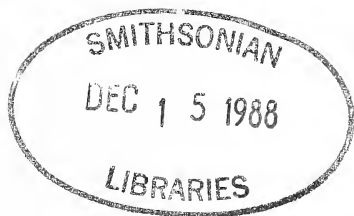
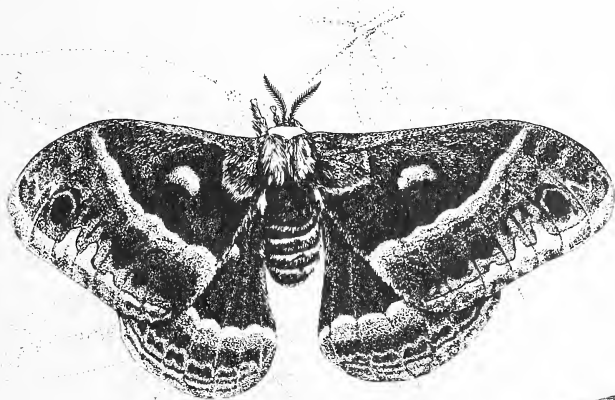
# LEPIDOPTERISTS' SOCIETY

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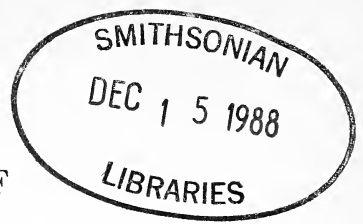
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**Cover illustration:** Captive female cecropia moth, *Hyalophora cecropia* (L.) (Saturniidae), released to wild and resting on staghorn sumac, *Rhus typhina* L. (Anacardiaceae). Submitted by Monica Miller, 5560 Library Road #201, Bethel Park, Pennsylvania 15102.



# JOURNAL OF THE LEPIDOPTERISTS' SOCIETY

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## SYSTEMATIC POSITIONS OF *ACENTRIA EPHEMERELLA* (DENIS & SCHIFFERMÜLLER), NYMPHULINAE, AND SCHOENOBIIINAE BASED ON MORPHOLOGY OF IMMATURE STAGES (PYRALIDAE)

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**ABSTRACT.** *Acentria ephemerella* (Denis & Schiffermüller), the one known species of its genus, is sometimes placed in Schoenobiinae, but it lacks three important autapomorphies of that subfamily: larval prothoracic sac, exposed pupal mesothoracic coxae, and deep pitlike pupal mesothoracic spiracle. Apomorphies such as spinelike pupal frontal setae, lack of pupal mesothoracic spiracle, and reduced posterior pupal abdominal spiracles confirm that *Acentria* belongs in Nymphulinae. No larval or pupal characters were found to support *Acentria* as a separate family or subfamily (Acentropidae or Acentropinae). Several synapomorphies suggest Nymphulinae and Schoenobiinae are sister groups. They share long exarate pupal appendages and reduction of larval L2 seta on abdominal segments 1-8. The unisetose L group on abdominal segment 9 in other subfamilies of Crambiformes may be used as a synapomorphy to define a clade separate from Nymphulinae and Schoenobiinae in which the L group is bisetose on segment 9.

**Additional key words:** larva, pupa, cladogram, systematics.

*Acentria ephemerella* (Denis & Schiffermüller), formerly *Acentria* (= *Acentropus*) *nivea* (Olivier), has a long and varied systematic history (Speidel 1981, 1984). It was placed in Schoenobiinae because of a reduced proboscis, tubular CuP (1A) forewing vein, and lack of hindwing Cu pecten (hair fringe) (Hampson 1895, Forbes 1926, 1938). Other workers (Marion 1954, Roesler 1973, Leraut 1980, Goater 1986) thought *Acentria* should be in Acentropinae or Acentropidae largely because the adult lacks a praecinctorium. Nigmann (1908) and Speidel (1981) cited enlarged anterior abdominal pupal spiracles as an autapomorphy of Nymphulinae and thus considered *Acentria* to be in this subfamily because of its similar pupa. Larval chaetotaxy confirmed this view. Hasenfuss (1960) placed *Acentria* in Nymphulinae based on a bisetose L group on abdominal segment 9, and unusual arrangement of larval



stemmatal (ocular) setae. Speidel (1984) suggested *Acentria ephemerella* is the correct name for *A. nivea* and recommended acceptance of Acentropinae instead of Nymphulinae as the valid subfamily name. The latter change, in agreement with Minet (1982), is not followed here because Nymphulinae has been stable and unambiguous in most checklists. Fletcher and Nye (1984) placed *Acentria* with Nymphulinae in their Pyraloidea catalogue. However, Yoshiyasu (1985) doubted the placement of *Acentria* with Nymphulinae because enlarged abdominal spiracles are also found in some aquatic Crambinae. The possibility remained that enlarged spiracles had arisen in certain species because of aquatic habits instead of common ancestry. Minet (1982, 1985) also considered *Acentria* to be a nymphuline, based on several apomorphies of the tympanum. As was traditional in the U.S., Munroe (1983) listed *Acentria* with Schoenobiinae. Batra (1977), Berg (1942), Buckingham and Ross (1981), Speidel (1981), and Yoshiyasu (1985) either illustrated stages of *A. ephemerella* or discussed its biology.

Only three workers have published Pyralidae cladograms (Fig. 1). Roesler (1973), relying mostly on adult morphology, recognized an Acentropidae-Crambidae complex. Yoshiyasu (1985) doubted the validity of Roesler's characters. He called attention to variability in the Nymphulinae radial vein and maxillary palpi, as well as to the presence of aquatic species in other subfamilies. More importantly, some key portions of Roesler's (1973) cladogram are defined by plesiomorphic features (lack of specialized scales in the male genitalia, for example). Kuznetsov and Stekolnikov (1979) considered Schoenobiinae and Nymphulinae to be unrelated, based almost exclusively on genital musculature. However, they studied very few species and paid only superficial attention to immature stages. Yoshiyasu (1985), considering characters of all stages, linked Schoenobiinae, Nymphulinae, and *Acentria* as sister groups but was unable to place this clade in an overall scheme. Instead, three clades were extended to a single point with dotted lines and a question mark at their bases (Fig. 1A). Thus, convincing evidence from adult (Minet 1982), larval (Hasenfuss 1960) and pupal (Nigmann 1908) morphology suggests *Acentria* belongs with Nymphulinae in spite of recent doubts (Yoshiyasu 1985, Goater 1986).

This paper examines apomorphic larval and pupal characters of *Acentria ephemerella* to provide additional evidence on the systematic position of *Acentria*. The relation of Nymphulinae to Schoenobiinae, and their taxonomic position within Crambiformes are also discussed.

#### METHODS

Morphological information on pyralid immature stages came from Passoa (1985), literature illustrations, and borrowed material. Unpub-

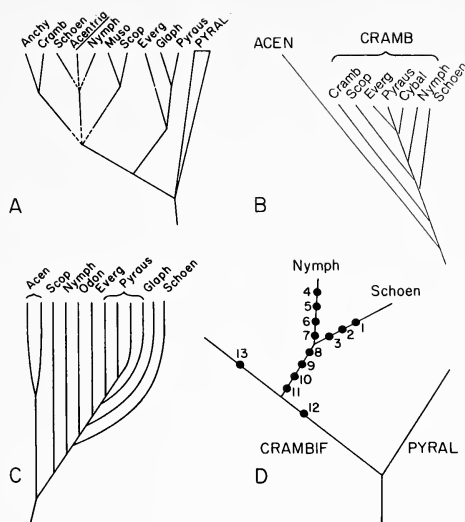


FIG. 1. Systematic position of *Acentria*, Nymphulinae, and Schoenobiinae after various authors. A, Yoshiyasu (1985). B, Roesler (1973). C, Kuznetsov & Stekolnikov (1979). D, Present study, with major apomorphies numbered as follows: 1—larva with prothoracic sac; 2—pupal mesothoracic spiracle pitlike; 3—pupal mesothoracic coxae exposed; 4—stemmata setae in line with each other; 5—pupal frontal setae enlarged and spinelike; 6—pupal anterior abdominal spiracles enlarged and on conelike projections, posterior abdominal spiracles reduced; 7—pupal mesothoracic spiracle lost; 8—V1 lost on larval thorax; 9—L2 on larval abdominal segments reduced; 10—tegumen-vinculum plate developed, transtilla lost; 11—pupal appendages exarate with metathoracic legs exposed; 12—praecinctorium present; 13—larva with unisetose L group on A9. Abbreviations: ACEN—Acentropinae; Acen—Acentropinae; Anchy—Ancyrolomiinae (Ancyrolomiinae of Yoshiyasu 1985); CRAMB—Crambidae; Cramb—Crambinae; CRAMBIF—Crambiformes; Cybal—Cybalomiinae; Ever—Evergestinae; Glap—Glaphyriinae; Muso—Musotiminae; Nymph—Nymphulinae; Odon—Odontinae; PYRAL—Pyralliformes; Pyraus—Pyraustinae; Schoen—Schoenobiinae; Scoop—Scopariinae.

lished keys and a data matrix of larval characters by workers at the U.S. National Museum (C. Heinrich, H. Capps, and D. Weisman) ("USNM Tables") provided information on pyralid genera in that collection. Literature on Crambiformes immature stages included general works such as Fracker (1915), Mosher (1916), Peterson (1962), and Neunzig (1987) for the U.S., Hasenfuss (1960) for Europe, Nakamura (1981) for Asia, and Gerasimov (1947, 1949) for the U.S.S.R. Important articles on New World Nymphulinae immatures were selected from Munroe (1981, 1982). Yoshiyasu (1985) published a review on Japanese Nymphulinae and their systematic position. Schoenobiinae immatures were discussed by Passoa and Habeck (1987). Crawford (1961), Mauston (1970), and Tan (1984) provided descriptions of Crambini larvae and pupae. Agarwal and Chaudhry (1966), Passoa (1985), and Rothschild (1967) described Chilini immatures. Works on New World Pyraustinae

included Allyson (1981, 1984), and Passoa (1985). Khot'ko and Molchanova (1975) studied Old World species. Some African pyralids were illustrated by Breniere (1979). Indian pyralids were described by Mathur and Singh (1963) and Mathur (1954, 1959).

Preserved larvae, and usually pupae, of the following species were examined:

#### Nymphulinae

<i>Acentria ephemerella</i> (Denis & Schiffermüller)	<i>Neargyractis slossonalis</i> (Dyar)
<i>Nymphula depunctalis</i> Guenée	<i>Petrophila longipennis</i> (Hampson)
<i>N. fluctuosalis</i> (Zeller)	<i>P. bifascialis</i> (Robinson)
<i>Munroessa</i> sp.	<i>P. avernalis</i> (Grote)
<i>Synclita</i> sp.	<i>P. jalscalis</i> (Schaus)
<i>Parapoinx diminutalis</i> Snellen	<i>Utingeriessa onyxalis</i> (Hampson)
<i>P. obscuralis</i> (Grote)	<i>Eopargyractis</i> sp.

#### Schoenobiinae

<i>Rupela albinella</i> (Cramer)	<i>Scirpophaga</i> (=Schoenobius, Tryporyza)
<i>R. horridula</i> Heinrich	<i>incertulas</i> (Walker)
<i>R. leucate</i> (Zeller)	<i>S. excerptalis</i> (Walker) (=S. <i>intacta</i> Snellen)
<i>R. sp.</i>	<i>Donacaula</i> sp.
	<i>D. maximella</i> (Fernald)

This list represents 9 of 16 Nymphulinae genera and 3 of 5 Schoenobiinae genera in the U.S. (Munroe 1983). *Acentria* contains only one species, *A. ephemerella* (Speidel 1984). Larva and pupa terminology follows Stehr (1987) and Mosher (1916). Munroe (1972) and Minet (1982, 1983, 1985) were used to characterize adult subfamilies.

#### CHARACTER POLARITY

Certain assumptions are necessary before a cladistic study of *Acentria*, Nymphulinae, and Schoenobiinae can proceed. Pyralidae is assumed monophyletic because of apomorphies in the tympanum (Minet 1982, 1983, 1985) and venation (Munroe 1972). All Pyralidae cladograms (Fig. 1) agree there are two lineages, Crambiformes (sometimes called Crambidae) and Pyraliformes (sometimes called Pyralidae in a restricted sense). Crambiformes, which include Nymphulinae, Schoenobiinae, and *Acentria*, are apomorphically defined, in part, by a praecinctorium in the tympanum (Minet 1982). Although tympanic morphology of Midiliformes and other pyralids differ, larval characters, as discussed further on, support Minet's (1982) placement of this taxon within Crambiformes. Pyraliformes, which include all remaining pyralid subfamilies, are the sister group to Crambiformes, and thus comprise the outgroup. Minet (1985) apomorphically defined Pyraliformes by a tympanic "paraspina" and sclerotized pinaculum rings around

larval seta SD1. Speidel (1984) mentioned scale morphology, dimorphic labial palps, and reduction of proboscis, ocelli, and leg spurs as apomorphies of *Acentria*. A shortened, stout gnathos, and broad basal portion of the apophysis united *Acentria* and *Kasania* on a single clade.

Unless stated otherwise, Watrous and Wheeler's (1981) method of outgroup comparison was used to polarize characters. This method is especially appropriate when most characters have two states, and relatives are easily defined. In spite of criticisms (Farris 1982, Clark & Curran 1986), outgroup comparison appears to be the most reliable way to determine polarity (Donoghue & Cantino 1984). All morphological features relevant to the systematic positions of *Acentria*, Nymphulinae, and Schoenobiinae are mentioned below even if their polarity is somewhat uncertain. References under each morphological feature usually provide illustrations.

### Larval Characters

**Stemmatal (ocular) setae.** Hinton (1946) considered S1 close to stemmata 3 and 4, S2 level with stemma 5, and S3 below all stemmata as the usual arrangement in Lepidoptera. This trend is also true in Pyralidae where all Pyraliformes and Crambiformes except Nymphulinae show this arrangement (Hasenfuss 1960, Yoshiyasu 1985). Two states occur in Crambiformes: setae in nonlinear arrangement or in line with each other. Since all Pyraliformes (the outgroup) have a nonlinear arrangement, this is considered plesiomorphic. The alternative state in Crambiformes, stemmatal setae in a line with each other, is apomorphic.

**Mandible.** Based on study of Pyralidae mandibles (Passoa 1985, Neunzig 1987, Peterson 1962), presence of a dentate ridge under the first scissorial tooth is an unusual modification. Inner teeth are sometimes present on the first molar ridge, especially in Pyraustinae (Peterson 1962, Passoa 1985), but in the latter case they do not form a ridge. Two character states occur in Crambiformes: ridge absent or present. Since all Pyraliformes lack a ridge (Passoa 1985), this is plesiomorphic. A dentate ridge, the alternative state, is apomorphic.

**Thoracic V1 seta.** Hinton (1946) stated V1 was present on all first and last instar Lepidoptera he examined. In Crambiformes, two character states occur: V1 absent (Yoshiyasu 1985) or present (Passoa 1985). Since V1 is present in Pyraliformes (Passoa 1985), this is plesiomorphic. Therefore, loss of this seta is considered apomorphic.

Rothschild (1967) speculated V1 may not be lost in *Tryporyza* (Schoenobiinae) but instead could have migrated to the coxae as in some Tineidae and Psychidae (Hinton 1946). The extreme reduction in body setal length of Nymphulinae and Schoenobiinae (setae may be difficult to see even under a compound microscope), coupled with lack of knowledge about coxal setae and their homologies, makes evaluation of Rothschild's hypothesis impossible at present. In any event, either case would be apomorphic as V1 is not found on the coxa in the outgroup (Pyraliformes).

**Prothoracic membranous sac.** The Schoenobiinae membranous sac is apparently a unique structure not homologous to other lepidopteran cervical glands (Passoa & Habeck 1987). In Crambiformes, two character states occur: prothoracic sac present or absent. All Pyraliformes lack a prothoracic sac (Passoa 1985). Therefore, presence of a membranous prothoracic sac is apomorphic.

**L2 seta on abdominal segments.** Hinton (1946) remarked that L1 and L2 are macroscopic and frequently subequal in length throughout Lepidoptera. This is true for all Pyraliformes and Crambiformes except Schoenobiinae (Hasenfuss 1960) and Nymphulinae (Neunzig 1987, Yoshiyasu 1985). Therefore, when L1 and L2 are subequal in length, this is plesiomorphic. A very short, almost microscopic, abdominal L2 seta is apomorphic.

**Thoracic L seta.** Neunzig (1987) noted that all Pyraliformes have three setae in the L group of mesothorax and metathorax. In Crambiformes, two character states occur: L group bisetose (some Nymphulinae and Schoenobiinae) or L group trisetose (most Crambiformes). Therefore, loss of the thoracic L seta is considered apomorphic.

**L2 on A9.** All Pyraliformes have L1, L2, and L3 present on A9, whereas L2 is either present (Schoenobiinae and Nymphulinae) or absent (most Crambiformes) in other pyralid larvae (Neunzig 1987, Hasenfuss 1960). L1 is always present in Pyralidae while L3 is always absent in Crambiformes. Because outgroup comparison demands a character distribution in which a feature is present or absent in the group being studied, L2 is the only seta that can be polarized at present. Since L2 is present in the outgroup, the plesiomorphic state within Crambiformes occurs when L2 is present (bisetose condition). In contrast, the apomorphic state occurs when L2 is lost (unisetose condition).

Yoshiyasu (1985) also considered loss of L setae in Crambiformes to be apomorphic but he polarized both bisetose and unisetose conditions as apomorphies. Unfortunately, this idea cannot be confirmed by outgroup comparison until more information is available on the sister group of Pyralidae. If the unisetose condition is apomorphic, the bisetose condition may be part of a trend from trisetose (plesiomorphic state) to a unisetose L group on A9.

**Extra pinacula.** When present, pinacula are located only around setal bases in Pyraliformes and most other Lepidoptera (Hinton 1946, Passoa 1985). In Crambiformes, two character states occur. There may be extra pinacula (apparently lacking setae) on the thorax and abdomen of Crambinae, a few Pyraustinae, and Scopariinae (MacKay 1972, Passoa 1985) while extra pinacula are absent in Nymphulinae and Schoenobiinae. Therefore, development of secondary pinacula is considered apomorphic. When extra pinacula are lacking, this is plesiomorphic.

## Pupal Characters

**Frontal setae.** Frontal setae are about as thick as other body setae in Pyraliformes (Passoa 1985). In Crambiformes, they are thin in all subfamilies except Nymphulinae (Passoa 1985) and several described Musotiminae (Nakamura 1977, for example). Therefore, thin setae are plesiomorphic while thick spinelike frontal setae are apomorphic.

**Mesothoracic spiracle.** Outgroup comparison is of limited value here since both clades have equal character distributions. In Pyraliformes, all subfamilies except Galleriinae and some Phycitinae have a mesothoracic spiracle (Passoa 1985). Among Crambiformes, all subfamilies except Nymphulinae have a mesothoracic spiracle. Loss of the mesothoracic spiracle is considered apomorphic by parsimony since three independent losses (Nymphulinae, Galleriinae, and some Phycitinae) is a more likely evolutionary scenario than independent gain of this spiracle many times in other pyralid subfamilies. Moreover, Mosher (1916) found a mesothoracic spiracle on nearly all other Lepidoptera studied. This supports the contention that a mesothoracic spiracle was probably present in ancestors of Pyralidae.

No Pyraliformes examined during this study have a deep pitlike mesothoracic spiracle. In Crambiformes, all subfamilies except Schoenobiinae lack a deep pit. Therefore, a pitlike mesothoracic spiracle is considered apomorphic while absence of a pitlike mesothoracic spiracle is plesiomorphic.

It should be noted that some Pyraustinae (for example, *Spoladea* and *Asciodes*) have pits adjacent to the mesothoracic spiracle while a few Epipaschiinae have the spiracle set in a shallow concavity. This should not be confused with the situation in Schoenobiinae where only a deep pit can be found and no trace of the spiracle is visible inside the pit.

**Anterior abdominal spiracles on A1-3.** All Pyraliformes lack enlarged anterior abdominal spiracles set on conelike projections (Passoa 1985). In Crambiformes, two character states exist. Nearly all species of Crambiformes except Nymphulinae (Speidel 1984) and *Thopeutis forbesellus* (Fernald) (Crambinae) lack enlarged anterior abdominal spiracles set on conelike projections. Therefore, lack of enlarged anterior abdominal spiracles is plesiomorphic while their presence on conelike projections is apomorphic. Speidel (1981)



also considered enlarged anterior abdominal spiracles of Nymphulinae pupae to be apomorphic.

**Posterior spiracles.** All Pyraliformes examined during this study have anterior and posterior spiracles subequal in diameter. In Crambiformes, two character states exist. Most species, except Nymphulinae and a few Pyraustinae, have spiracles subequal in diameter throughout the abdomen. This is considered plesiomorphic. Reduced posterior spiracles are considered apomorphic.

**Mesothoracic and metathoracic coxae.** All Pyraliformes and all Crambiformes except Schoenobiinae have hidden mesothoracic and metathoracic coxae. Thus, exposed mesothoracic and metathoracic coxae are apomorphic while hidden coxae are plesiomorphic. Davis (1986) noted that only the forecoxa is exposed in higher Lepidoptera, and thus he considered exposed mesothoracic coxae to be apomorphic.

**Metathoracic legs.** All Pyraliformes have obdact appendages; the metathoracic legs, if not hidden, have only their tips exposed. This is also true of most Crambiformes, except Nymphulinae and Schoenobiinae which have exarate appendages with metathoracic legs clearly exposed. Fully exposed metathoracic legs and exarate appendages are considered apomorphic while partially hidden metathoracic legs are plesiomorphic.

### Adult Characters

**Proboscis.** Most pyralids have the proboscis well developed and scaled but some Crambiformes (Schoenobiinae) and Pyraliformes (Peoriinae) lack a proboscis (Munroe 1972). This character distribution (present or absent in each clade) limits the usefulness of outgroup comparison. Instead, a reduced proboscis is considered apomorphic by parsimony since two independent reductions are more likely than many acquisitions.

**Forewing CuP.** Forewing CuP is another difficult character to polarize by outgroup comparison since it may be either a fold or a tubular remnant in each clade of Pyralidae (E. G. Munroe pers. comm.). Perhaps a fully developed vein was gradually lost until only a tubular remnant remained at the distal end of the forewing. This reduction of CuP continued so only a fold now marks its former position. Since Common (1970) noted a trend in higher Lepidoptera where anal and radial veins are gradually lost in advanced forms, reduction of CuP to a fold is tentatively called apomorphic. Further studies on Pyraloidea ancestors would help polarize this character, but Dugeoneids, which Minet (1982) believed could be the sister group of the Pyralidae, have CuP developed.

Another possibility, independent reacquisition of CuP in Schoenobiinae, some Nymphulinae and some Pyraliformes, is equally parsimonious with the reduction of CuP in most Crambiformes, most Pyraliformes, and some Nymphulinae. CuP reduced to a fold would be plesiomorphic while gain of a tubular remnant would be apomorphic. This polarization of CuP is especially attractive if morphological studies show the sister group of Pyralidae is not Dugeoneidae (dugeoneids have CuP developed).

**Praecinctorium.** The praecinctorium is either present (Crambiformes) or absent (Pyraliformes) in Pyralidae. Dugeoneidae, a tentative sister group of Pyralidae, lacks a praecinctorium. Thus, presence of a praecinctorium is apomorphic whereas its absence is plesiomorphic.

*Acentria* probably lost the praecinctorium secondarily because it may be vestigially present in the tympanum (Minet 1985). Given presence of a praecinctorium as a ground-plan apomorphy of Crambiformes, absence or extreme reduction of praecinctorium must be an apomorphic reversal.

**Tegumen-vinculum plate.** All Pyraliformes lack the t-v plate (Yoshiyasu 1985). This is also true for all Crambiformes except Nymphulinae and Schoenobiinae (Yoshiyasu 1985). Therefore, presence of the t-v plate is considered apomorphic.

**Cu hindwing pecten.** Munroe (1972) noted that cubital pecten occurs in both Crambiformes and Pyraliformes, and this limits outgroup comparison as a method of analysis. However, parsimony would indicate that several independent gains of cubital pecten are more likely than numerous losses. This suggests that presence of pecten is apomorphic while its absence is plesiomorphic. Roesler (1973) also considered presence of pecten to be apomorphic.

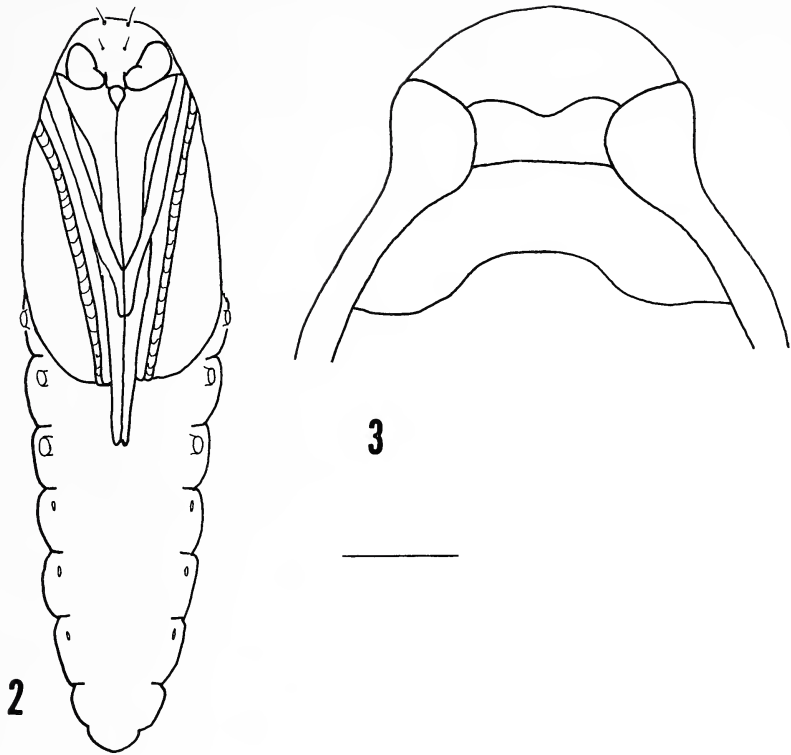
## BIOLOGY

**Aquatic habitat.** Nearly all Pyraliformes are terrestrial, and do not form cases entirely of leaf fragments. This is true of all Crambiformes except Nymphulinae. When restricted to exclude Musotiminae, Nymphulinae include species which are always aquatic and frequently form cases. Thus, aquatic habit is apomorphic while terrestrial living is plesiomorphic. Speidel (1981) also considered aquatic living to be apomorphic.

TAXONOMIC AFFINITIES OF *ACENTRIA*

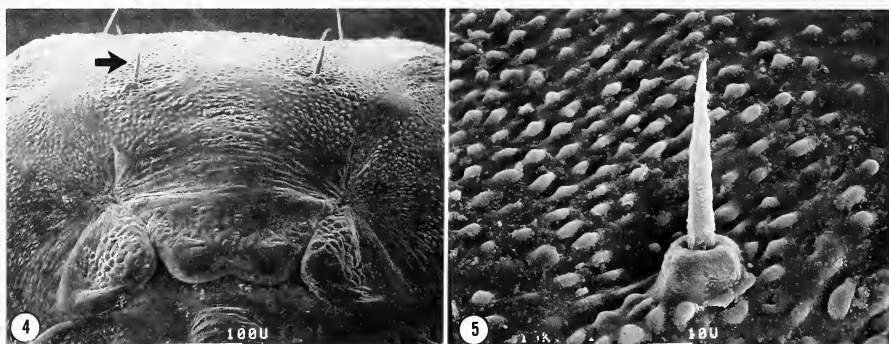
The above characters and their polarities provide additional information on the systematic position of *Acentria ephemerella*. Schoenobiinae larvae are apomorphically defined by a membranous prothoracic sac (Hasenfuss 1960, Passoa & Habeck 1987), which is absent from *Acentria* (Yoshiyasu 1985). *Acentria* also lacks the pitlike mesothoracic spiracle and exposed mesothoracic coxae (Figs. 2, 3) that apomorphically define Schoenobiinae pupae (Passoa & Habeck 1987). Therefore, immature stages of *Acentria* demonstrate the genus is misplaced in Schoenobiinae. Hampson (1895) and Forbes (1938) claimed affinity between *A. ephemerella* and Schoenobiinae because of a reduced proboscis, tubular forewing CuP, and absence of hindwing cubital pecten. Lack of cubital pecten is plesiomorphic; thus absence of this feature does not indicate relation (individuals sharing symplesiomorphies may not be relatives). The tubular forewing CuP may be apomorphic, but this character is found in both Nymphulinae and Schoenobiinae (Munroe 1972), and thus does not clarify the systematic position of *Acentria*. The single apomorphic adult character that *Acentria* and Schoenobiinae have in common, a reduced proboscis, perhaps arose through convergence since both taxa are associated with a similar (moisture-rich) aquatic environment. Although a reduced proboscis is usually considered characteristic of Schoenobiinae (Forbes 1938), some Nymphulinae also have the proboscis reduced (Yoshiyasu 1985), so a species with reduced mouthparts could be a member of either subfamily. Adult morphology, like that of immatures, provides little evidence that *Acentria* belongs in Schoenobiinae.

As mentioned earlier, there may be strong selection for enlargement of anterior abdominal spiracles in pupae of aquatic pyralids. These spiracles were considered autapomorphic for Nymphulinae (Speidel 1984), but they also occur in some aquatic Crambinae of Asia (Yoshiyasu 1985), *Thopeutis forbesellus* (Fernald) of the United States, and a few terrestrial Pyraustinae genera such as *Lygropia*, *Microthyris*, *Spoladea*, and *Marasmia* (Passoa 1985). Nevertheless, other pupal apomorphies indicate *Acentria* is related to Nymphulinae. Enlarged spinelike frontal setae are found on most Nymphulinae pupae (Yoshiyasu 1985), and are apomorphic for this subfamily. *Acentria* has these enlarged setae (Figs.



FIGS. 2, 3. **2**, Ventral view of *Acentria ephemerella* pupa. Scale line = 0.8 mm. **3**, Dorsal view of *Acentria ephemerella* pupal antenna and thorax. Scale line = 0.25 mm.

4, 5) which indicates a close relation to Nymphulinae. In addition, very few pyralid subfamilies (Galleriinae, Nymphulinae, and some Phycitinae) lack a mesothoracic spiracle (Passoa 1985). Among Crambiformes, only Nymphulinae show this loss. *Acentria* has no mesothoracic spiracle (Fig. 3) and, as is typical for Nymphulinae, has enlarged anterior abdominal spiracles set on conelike projections (Fig. 2). This spiracular arrangement, when combined with much reduced posterior spiracles, is autapomorphic for Nymphulinae. *Thopeutis forbesellus* (Crambinae) has anterior abdominal spiracles set on weak conelike projections, but the abdominal spiracles are all equal in diameter. Some Pyraustinae have enlarged anterior abdominal spiracles (Passoa 1985), but unlike Nymphulinae, lack conelike projections and have posterior spiracles at least half the diameter of anterior ones. These examples show, as Yoshiyasu (1985) suspected, that convergence has produced enlarged spiracles and conelike projections in other Crambiformes.



FIGS. 4, 5. 4, Micrograph of *Acentria ephemerella* labrum, pillifers, frons, and vertex. Arrow points to spinelike frontal seta. Scale line = 100 microns. 5, Micrograph of *Acentria ephemerella* spinelike frontal seta. Scale line = 10 microns.

However, it still remains possible to define Nymphulinae pupae easily by their frontal setae and other spiracular modifications.

Besides the aquatic habit (Nigmann 1908) and stemmatal setal arrangement (Hasenfuss 1960), another larval apomorphy may help resolve the systematic position of *Acentria ephemerella*. Many Nymphulini have a dentate ridge on the mandible (Yoshiyasu 1985, "semicircular arrangement" of Lange 1956) which also occurs in *Acentria* (Yoshiyasu 1985). This contrasts with *Argyractini* larvae which have the mandible more elongated, flattened, and usually without the dentate ridge (Lange 1956). Other characters (Lange 1956, Speidel 1984) such as diet of submerged plants, prothoracic shield chaetotaxy, ability to make cases of leaf fragments, lack of gills on body, lack of palmate setae on labrum, and three enlarged pupal spiracles would indicate *A. ephemerella* lacks apomorphies of *Argyractini* and belongs in Nymphulini as defined by Lange (1956). Speidel (1984) did not use mandibles, pupal spiracles, or labral setae in his Nymphulinae cladogram. Since the tribal classification proposed by North American workers can be difficult to apply to certain Asiatic genera, for example *Nymphicula* (Yoshiyasu 1980), these features merit further attention.

In summary, *Acentria* is misplaced in Schoenobiinae because immature stages radically differ. In spite of some morphological specializations, there seems little reason to consider this genus separate from Nymphulinae. Placement of *Acentria* in its own family or subfamily was based, in part, on lack of a praecinctorium which is unusual among Crambiformes. Minet (1985), while studying the tympanum, found a possible praecinctorium vestige, and thus placed *Acentria* in Nymphulinae. No characters in immature stages were found to exclude *Acentria* from Nymphulinae as a separate taxon, although crochet arrangement



is somewhat unusual. Since differences between the tympanum of *Acentria* and other nymphulines may not be as great as previously thought, and several additional larval and pupal apomorphies confirm its relation to Nymphulinae and exclude it from known Schoenobiinae, there seems little doubt that transfer of *Acentria* to Nymphulinae by Hasenfuss (1960) was correct.

It is worth noting that *Neoschoenobia decoloralis* Hampson, another disputed taxon placed in Nymphulinae (Inoue 1982, cited by Yoshiyasu 1985) and Schoenobiinae (Lewvanich 1981), might be a member of Schoenobiinae because it has exposed pupal coxae and lacks enlarged pupal spiracles and stemmatal setae in a straight line. Since illustrations by Yoshiyasu (1985) do not show a mesothoracic spiracle or a larval prothoracic sac, it seems wise to retain this species in Nymphulinae, although preserved specimens should be examined for these features.

#### RELATION BETWEEN NYMPHULINAE AND SCHOENOBIIINAE

Historically, the systematic position of Schoenobiinae has been debated. Börner (cited by Munroe 1958) thought Crambinae and Schoenobiinae were close relatives. Roesler (1973) considered them unrelated based on maxillary palpi and cubital pecten. Kuznetsov and Stekolnikov (1979) included Crambinae, Schoenobiinae, and Nymphulinae as the most primitive members of their Crambidae.

Larval and pupal features indicate Crambinae and Schoenobiinae are not closely related phenetically or cladistically. Crambinae larvae have a unisetose L group on A9, and well developed extra pinacula on both thorax and abdomen (Passoa 1985, Tan 1984). Schoenobiinae larvae, in contrast, frequently have a bisetose L group on A9 and no pinacula (Passoa & Habeck 1987). Pupal structure is also radically different. Crambinae pupae either have a well developed cremaster (Crambini) or processes on the head or body (Chilini). Metathoracic legs are not exposed or are barely visible. Schoenobiinae pupae, in contrast, always have exposed metathoracic legs, and never have a cremaster or appendages on the head or body. In fact, it is difficult to find any synapomorphies in immature stages to link these two groups.

Immature stages do support the hypothesis of Passoa (1985) and Yoshiyasu (1985) that Schoenobiinae and Nymphulinae are related. Bollman (1955) and Allyson (1976) distinguished Schoenobiinae by their reduced L2 seta, but minute L setae are common on many Nymphulinae (Yoshiyasu 1985, Neunzig 1987). Additional apomorphies to unite Schoenobiinae and Nymphulinae include fully exposed metathoracic legs and exarate appendages. Other synapomorphies listed by Yoshiyasu (1985) are V1 lost on the larval thorax, and absence of transtilla with



development of the t-v plate in male genitalia. One exception is *Rupela albinella* (Passoa & Habeck 1987) which has V1 present, but this may merely represent a reversion to the primitive state. All other known species in both subfamilies lack V1, so loss of this seta is probably a groundplan apomorphy. Finally, several characters merit further investigation as synapomorphies of the Nymphulinae-Schoenobiinae clade. These are mesothoracic pupal spiracle (does the pit in Schoenobiinae contain a spiracle, or is the pit the spiracle itself); absence of pupal cremaster (unknown polarity); L setae of thorax bisetose (apomorphic but its distribution within the clade needs study); loss of pinacula (unknown polarity); and CuP tubular at margin (unknown polarity). In addition, a bisetose L group on A9 was thought characteristic of only Nymphulinae (Yoshiyasu 1985, Hasenfuss 1960, Bollman 1955) but this condition is also found in several Schoenobiinae genera (Passoa & Habeck 1987). Some illustrations show a unisetose L group on A9 in Schoenobiinae (Hasenfuss 1960) but these probably represent cases where L2 was overlooked. Chaetotaxy of Schoenobiinae larvae is difficult to study without slide mounts of larval skin. Further study may also show the bisetose L group on A9 is a synapomorphy of the two subfamilies.

#### RELATIONS OF NYMPHULINAE-SCHOENOBIIINAE CLADE IN CRAMBIFORMES

Relation of the Nymphulinae-Schoenobiinae clade to other subfamilies has been unclear. Yoshiyasu (1985) defined a clade uniting all Crambiformes, except Pyraustinae and its relatives, by a reduced transtilla. However, certain exceptions to this generalization limit its use as a synapomorphy. Yoshiyasu (1985) characterized Pyraustinae and Glaphyriinae by their well developed transtilla, but E. G. Munroe (pers. comm.) stated that the transtilla varies widely in these groups. One alternative to a clade defined by transtilla morphology, with far fewer exceptions, involves L setae on A9. The Nymphulinae-Schoenobiinae clade is separated from remaining Crambiformes by the number of L setae on A9. Other Crambiformes subfamilies, without exception, have a unisetose L group on A9 (loss of seta L2 is an apomorphy), which defines them as a monophyletic group. This seta is present (bisetose condition) in nearly all Nymphulinae (restricted sense) and Schoenobiinae larvae. Although the above phylogeny accepts some parallel evolution with the presence of a unisetose L group in a single Nymphulinae species (Yoshiyasu 1985) and in published figures of some Schoenobiinae (if these figures are correct), this represents only a very small number of species. Parallel evolution appears to be normal in the evolution of both Macrolepidoptera (Michener 1949) and Microlepi-

doptera (Kristensen 1984), so perhaps pyralids have also followed this trend. It seems unrealistic to expect a group with thousands of species to be defined by a single trait without parallelisms, so choice of a clade based on the L setae may represent the case with minimum homoplasy. Use of the unisetose L group on A9 as a synapomorphy supports Minet's (1982) contention that Midiliformes belong in Crambiformes since a *Midila* larva in the U.S. National Museum has a unisetose L group on A9. Moreover, separation of Musotiminae from Nymphulinae is supported by the fact that *Musotima* has a unisetose L group on A9 (Nakamura 1977) unlike the bisetose L group of other Nymphulinae (Hasenfuss 1960).

In conclusion, this study calls attention to the role of immature insects on Pyralidae classification and phylogeny. Modifications of pupae are especially diverse and in need of study. Future studies will probably use more larval and pupal characters, especially if the sister group of Pyralidae can be confirmed.

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## EFFECT OF LARVAL PHOTOPERIOD ON MATING AND REPRODUCTIVE DIAPAUSE IN SEASONAL FORMS OF *ANAEA ANDRIA* (NYMPHALIDAE)

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**ABSTRACT.** In experiments conducted under simulated field conditions in Baton Rouge, Louisiana, laboratory-reared summer-form female *Anaea andria* Scudder from 13- and 14-h larval photoperiods underwent oocyte maturation and mated within two days of eclosion. Laboratory-reared winter-form females from 13-h larval photoperiods did not mate, and showed little oogenesis 20 days after eclosion in simulated field conditions. Data from field-collected specimens numbering 55 winter forms and 26 summer forms support the experimental results, and indicate that female winter forms remain unmated and in reproductive diapause in the fall. Results suggest that larval daylength, by determining adult seasonal form, also regulates reproductive diapause and mating in *A. andria*.

**Additional key words:** Charaxinae, *Croton capitatus*, seasonal dimorphism.

*Anaea andria* Scudder (Nymphalidae: Charaxinae) is distributed from Texas to Nebraska, E to West Virginia, Georgia, and the Florida panhandle (Opler & Kriezek 1984). It is common in the southern Mississippi basin and Gulf Coast where it occurs with its primary host plant, *Croton capitatus* Michx. (Euphorbiaceae), an annual herb.

Adult *Anaea andria* are characterized by distinct seasonal wing dimorphism induced by larval photoperiod (Riley 1980, 1988). Winter-form butterflies emerging in fall and surviving until the following spring are characterized by apically acute and falcate forewings, well developed hindwing tails and anal angle projections, and brighter and more contrasting coloration than summer-form butterflies. Summer forms have non-falcate forewing apices, reduced tails and anal-angle projections on hindwings, and lighter overall coloration. Photoperiods of 14 h or more result primarily in summer-form adults. Decreasing photoperiods result in a greater percentage of winter-form individuals (Riley 1988).

In Louisiana, summer-form *A. andria* occurs from May to September when actively growing host plants are available. The winter form begins to appear in late August, and survives until June of the following year. Its appearance in the fall is followed shortly by the beginning of *Croton capitatus* senescence.

The occurrence of two distinct seasonal forms, one when food plants are abundant, and another when they are in decline, suggests that a corresponding difference in female reproductive status may also occur. In this paper, effects of larval daylength on reproductive diapause and

mating in laboratory-reared seasonal forms of *A. andria*, and the mating and reproductive status of field-collected seasonal forms are reported.

## METHODS

Experimental insects were collected in East Baton Rouge and East Feliciana parishes, Louisiana. Larvae were collected from host plants in the field, or reared from eggs deposited on container-grown host plants by reared and field-collected butterflies confined in 2-m<sup>3</sup> Saran® screen outdoor cages (Chicopee Manufacturing Co., Cornelia, Georgia 30531). Adults were collected using traps similar to those described by Rydon (1964) baited with bananas.

Larvae were reared in clear plastic 26 × 20 × 10-cm boxes containing a raised 3-mm mesh metal grid to prevent undue larval contact with feces. Larvae were fed fresh *Croton capitatus* leaves, and the boxes cleaned daily or as needed. Pupation occurred on tops and sides of the boxes and on plant material.

Seasonal forms of *A. andria* were produced by rearing the third instar in environmental chambers with controllable photoperiods. To obtain summer-form butterflies, 14 h of light was used. Winter and summer forms were obtained using a 13-h photoperiod. Temperature in the chambers was 27°C during the experiments.

Laboratory-reared males and females of each seasonal form were maintained in separate outdoor cages. Eight hours after eclosion, females were numbered with permanent ink on the underside of a hind-wing and released into the cages. Males were also caged eight hours after eclosion, and remained in the cages until death. Virgin females were always caged with males of equal or greater age.

Well-ripened bananas were provided for adult food. Cage location provided exposure to full sun 6 h/day. One cage corner was covered with plywood to provide a shaded resting area for the butterflies. The experiment was conducted from 1 June to 31 October 1986; consequently, insects were exposed to a changing natural photoperiod. Each seasonal form was caged during the time of year when each can be found in the field, summer forms from 1 June to 23 September, winter forms from 6 August to 31 October.

Stage of oogenesis, number of mature eggs, and mating status were determined by dissection and examination of the female reproductive system. Summer forms were dissected 2 and 3 days after eclosion, and winter forms 10 and 20 days after eclosion. Stage of oogenesis is described using a scale of 0–5, 0 denoting no evident oocyte development, and 5 the presence of mature eggs (further explained in Table 1). Insects were judged to be in reproductive diapause if oocyte development 10

TABLE 1. Percentage mated, stage of oogenesis, and number of mature eggs/female in 2- and 3-day-old mated and unmated laboratory-reared summer-form *A. andria* under simulated field conditions.

Age (days)	N	Percent mated <sup>1</sup>	Mean stage of oogenesis <sup>2,3</sup>	No. mature eggs/female	
				Mean <sup>3</sup>	Range
2	18	83.3a	4.1a	0.6a	0-4
3	44	90.9a	4.9b	44.2b	0-82

<sup>1</sup> Not significant according to Fisher's Exact Test.

<sup>2</sup> 0-5 scale. 0 = no visible oocyte formation; 1 = beginnings of oogenesis; 2 = slight enlargement of oocytes; 3 = some oocytes 50% mature; 4 = greater oocyte enlargement, no oocytes at median oviduct; 5 = mature oocytes at median oviduct.

<sup>3</sup> Means in columns followed by the same letter do not differ significantly according to *F*-test ( $P < 0.01$ ).

days after eclosion was rated  $<2.0$ . Mated status of females was determined by spermatophore presence in the bursa copulatrix.

Percentage mating was analyzed using Fisher's Exact Test; all other variables were subjected to analysis of variance (SAS Institute 1985).

Voucher specimens are in the Louisiana State University Entomology Museum.

## RESULTS

**Laboratory-reared butterflies.** Winter-form butterflies resulted only from the 13-h photoperiod. Twenty-seven females and 30 males were reared. Twelve females were dissected after 10 days, and 15 dissected after 20 days of caging with winter-form males. None of the female winter forms had mated, and none of their ovarioles showed any sign of oogenesis. No courtship behavior or mating attempts were seen. It was therefore concluded that winter-form females remain in reproductive diapause for at least 20 days after eclosion. Male mating behavior and female attractiveness may also be inhibited in winter forms.

Summer-form butterflies resulted from both photoperiods, 40 females and 41 males from the 14-h, and 22 females and 25 males from the 13-h. Comparison of summer-form data from both photoperiods indicates that oogenesis, number of mature eggs/female, and mating were not significantly affected by these larval photoperiods.

Age was the most important factor affecting stage of oogenesis and number of mature eggs per female in recently eclosed summer forms. Two-day-old females showed significantly less oogenesis ( $F = 31.51$ ;  $df = 1, 58$ ;  $P < 0.01$ ), and carried fewer mature eggs ( $F = 59.18$ ;  $df = 1, 58$ ;  $P < 0.01$ ) than 3-day-olds (Table 1). The age  $\times$  photoperiod interaction was not significant.

Percentage of mated 2- and 3-day-olds did not differ (Table 1). In several instances, courtship of virgin females was observed within hours of their release into the outdoor cage. Although age of the males involved

was not known, it was concluded that mating behavior of male and female summer forms is not suppressed in recently eclosed butterflies. These observations suggest that most female summer forms are mated within a few days of emergence.

Among unmated summer forms, four were three days old, and three were two days old. Mean number of mature eggs/female for the 3-day-olds was 23.5 (range 0–48) while none of the 2-day-olds contained mature eggs, evidence that oogenesis in summer forms progresses with age, independent of mating.

**Field-collected butterflies.** Forty-two winter-form females were trapped during September–November 1984 and September 1985. They showed little evidence of oogenesis, and all were unmated (Table 2). Thirteen overwintered winter forms trapped in April and May 1985 were mostly mated and contained fully mature eggs (Table 2).

Summer-form females, collected in September 1984 and June to mid-September 1985, all carried fully mature eggs and all were mated (Table 2).

#### DISCUSSION

Laboratory results and field observations indicate that newly eclosed summer-form females undergo rapid oogenesis and are mated within two days of emergence. This enables summer forms to immediately begin ovipositing and larvae to complete development before onset of unsuitable environmental conditions. Conversely, winter-form females remain unmated and in reproductive diapause for a considerable time after adult eclosion. They are thus relieved of the physiological burden of producing and carrying mature or maturing eggs when environmental conditions are not favorable for oviposition and larval development. Reproductive status appears to be linked to adult seasonal form since summer forms from both 13- and 14-h photoperiods underwent rapid oogenesis while winter forms from the 13-h photoperiod remained in diapause.

Field observations of courtship, mating, and feeding behavior in *A. andria* support these conclusions (unpubl. data). No courtship activity has been seen in winter forms during fall. However, newly eclosed male and female winter forms are readily attracted to fermented fruit baits, indicating a possible feeding response linked to preparation for overwintering. In spring, winter-form males have been observed exhibiting strong territorial behavior, chasing other males, patrolling along forest edges and then returning to the same perch, engaging in courtship behavior, and attempting to mate with females. Baits placed near male territories and perches in spring have proven relatively unattractive and trapping ineffective. These observations lend support to the ex-

TABLE 2. Collection month, percentage mated, and stage of oogenesis in female *A. andria* collected 1984–85 in East Baton Rouge and East Feliciana parishes, Louisiana.

Month collected	Seasonal form	N	Percent mated	Mean stage of oogenesis <sup>1</sup>
September	Winter	18	0.0	0.0
October	Winter	23	0.0	0.5
November	Winter	1	0.0	1.5
April	Winter <sup>2</sup>	5	80.0	5.0
May	Winter <sup>2</sup>	8	100.0	5.0
June though September	Summer	26	100.0	5.0

<sup>1</sup> Same scale as in Table 1.<sup>2</sup> Overwintered butterflies.

perimental results and suggest different behavioral priorities in winter forms before and after overwintering. Factors initiating oogenesis and mating in winter forms that have overwintered are unknown.

My experience with bait traps during summer in Louisiana and Missouri, and that of Vernon Brou, Abita Springs, Louisiana, who operates bait traps year-round, indicate that summer forms are both trapped and collected less frequently than winter forms. They are also less common in collections. The total number of field-collected summer forms in collections of the author, V. Brou, and the Louisiana State University Entomology Museum is 77 compared to 241 winter forms (Riley 1988). This discrepancy may be due to collecting bias, but may also indicate greater behavioral priority for reproduction vs. feeding in summer forms, similar to winter-form behavior in the spring. These observations along with the experimental results suggest that larval daylength, by determining adult seasonal form, is also a major factor regulating mating and reproduction in recently emerged *A. andria*.

Photoperiod is well documented as a diapause inducing and regulating stimulus for insects (Beck 1980, Danilevsky et al. 1970, Tauber et al. 1986). It is an ideal environmental cue for *A. andria*. The nymphalid *Polygona c-aureum* L. is very similar in its response to daylength (Hidaka & Aida 1963, Fukuda & Endo 1966, Endo 1970, 1972). In *P. c-aureum*, reproductive diapause and seasonal wing dimorphism are determined by photoperiod but are under independent neuroendocrine control. Pheromone production and mating receptivity of female *P. c-aureum* are also hormonally regulated and under photoperiodic control (Endo 1973). The results presented here suggest that a similar interaction between daylength and neuroendocrine system could be controlling wing dimorphism, diapause, and mating in *A. andria*.

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# SYSTEMATIC STATUS AND DISTRIBUTION OF THE LITTLE-KNOWN CHARAXINE *PREPONA WERNERI* HERING & HOPP

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**ABSTRACT.** *Prepona weneri*, hitherto of uncertain systematic status, and since 1925 recorded from only the holotype male, is authenticated from eight additional specimens. Genitalia dissection and review of characters defining *Archaeoprepona* Fruhstorfer and *Prepona* Boisduval indicates *weneri* belongs in *Prepona sensu stricto*. Most specimens are from hydric forest habitat in the Chocó and Cauca areas of endemism, Colombia, but one has data indicating occurrence southward in the upper Rio Putumayo region. The disjunct distribution is probably relict, reflecting former wider occurrence of per-humid biomes.

**Additional key words:** Apaturidae, *Archaeoprepona*, Neotropics, biogeography.

Of all "Prepona" butterflies, *P. weneri* Hering & Hopp (1925) has been the most problematical. Previously recorded only from the holotype male (Hering & Hopp 1925, Le Moult 1932-33), its melanic appearance, unusual under-surface wing pattern, and hitherto unexamined genitalia have made it a taxon of uncertain status. The most recent treatment of Neotropical Nymphalidae (D'Abrera 1987) does not mention the species. From fieldwork and survey of public and private collections, we recently located eight additional specimens of *P. weneri*. Only two of these were collected since 1929, and it appears unlikely that more specimens will soon be available for study. We therefore summarize below our current determinations of the taxonomic status, biology, and biogeography of this seldom-collected charaxine butterfly.

## Taxonomy of "Prepona" Butterflies

Despite accumulation of specimens in private and public collections, there has not been wide agreement on the systematics of "Prepona" butterflies. Because of overall similarity in the striking blue and black markings of the wing upper surfaces, many authors have treated "Prepona" as a monophyletic group (Comstock 1944, Barcant 1970, Brown & Heinemann 1972, Riley 1975). However, as early as 1915, Fruhstorfer defined two subgroups of "Prepona". One he described as genus *Ar-*

*chaeoprepona* (type species *demophon* Linnaeus) (Fig. 2C), which he regarded as "primitive" (Fruhstorfer 1915). The other, including taxa placed with Boisduval's (1836) *Prepona* (type species *demodice* Boisduval) (Fig. 2D), he noted as sharing all morphological characters with *Agrias* Doubleday, from which it differed only in wing pattern. Le Moult (1932-33) also noted the heterogeneity of the group and proposed *Pseudoprepona* (type species *demophon* L., a junior objective synonym of *Archaeoprepona*). The above distinctions were followed by a number of authors (Orfila 1950, Rydon 1971, Descimon et al. 1973-74, Johnson & Quinter 1982).

As defined hitherto in the literature, some obvious phenetic differences separate *Archaeoprepona* from *Prepona* (Table 1). Authors recognizing these differences have considered both groups as genera (Stichel 1939, Papworth 1982) and even tribes (Rydon 1971) (Table 1). Our concern when considering the taxonomic status of *weneri* has been whether *Prepona* and *Archaeoprepona* are monophyletic groups. Our unpublished numerical cladistic analyses on taxa placed in these groups (Table 1), including outgroups *Charaxes*, *Polyura*, *Palla*, *Euxanthè* and Comstock's (1961) *Anaea sensu lato*, do not conflict with generic usage of *Prepona* and *Archaeoprepona* as reviewed in Table 1. Therefore, based on male genitalia (Fig. 2A, B) and historical usage, *P. weneri* can be reliably placed in *Prepona sensu stricto*.

*Prepona weneri* Hering & Hopp  
(Figs. 1A, B, C, 2A)

**Diagnosis. Male.** Upper surface of wings: ground darker black-brown than congeners, with blue stripes of deeper azure color (not silvery or blue-green) restricted thinly caudad the forewing discal cell and in a median arc across hindwing. Under surface of wings: hindwing with variably suffused median band, area basad discal band variously marked with dark blotches, two large eyespots each submarginal in cells RS and CuA1 (or a third in cell M3), forewing with disjunct or continuous apical and postmedian lines. **Genitalia** (Fig. 2A). Typical of general configuration of *Prepona sensu stricto* (Fig. 2D).

**Female.** Unknown.

**Distribution.** Principally Chocó and Cauca regions (region names follow areas of endemism postulated by Brown 1976, 1982), Colombia, with a single specimen having data indicating upper Putumayo region.

**Known specimens.** In addition to the type male (Zoologisches Museum der Humboldt Universität zu Berlin, ZMH), labelled "Origin, *Prepona weneri* Hering & Hopp, Rio Micay, Columbiën, Februar 1925, 1000m" (Fig. 1A, B, C), eight male specimens are reported here for the first time: (1) Rio Guayabal, Colombia, February 1929, anonymous private collection (examined by first author); (2) Rio Bravo, Prov. Valle, Colombia, March 1985, anonymous private collection (noted by collector as only specimen taken at locality in many years of collecting, examined by David Matusik, Field Museum of Natural History, FMNH, photograph examined by us); (3) Frontino, Colombia, no other data, anonymous private collection (photograph furnished to first author), one male; (4) Cisneros, Colombia, 6 May 1928 (purchased from Le Moult collection February 1968 for Niedhoffer collection), Milwaukee Public Museum (MPM) (photograph examined; genitalia dissected, illustrated in Fig. 2D); (5) Rio Micay, Cordillera Occidentale, Colombia,

TABLE 1. Main characters in literature differentiating *Archaeoprepona* and *Prepona*.

Character location (authors)	<i>Prepona</i>	<i>Archaeoprepona</i>
Wing upper surface (1-6)	Androconia well-defined, brush-like, with rigid setae	Androconia diffuse, softly hairy
Hindwing under surface (1-6)	Eyespots large, usually two, post-medial to marginal, cells RS and CuA1	Eyespots small, undifferentiated, marginal, cells RS to CuA2
Male genitalia (1, 3-5)	Slender in all parts (especially uncus and valvae); gnathos rod-like, with prominent radial spines	Stout in all parts; gnathos flat, without spines
Female genitalia (3, 7)	Sterigma Y-shaped	Sterigma circular

Taxa included: *Prepona amesta* Fruhstorfer, *brookiana* Godman & Salvin, *deiphile* Godart, *demodice* Godart, *dex-amenes* Herbst, *eugenes* Bates, *garleppiana* Staudinger, *gnorima* Bates, *laertes* Hübner, *omphale* Hübner, *pheridamas* Cramer, *praeneste* Hewitson, *pylene* Hewitson, *neoterpe* Hewitson, *xenagoras* Hewitson, *Archaeoprepona amphimachus* Fabricius, *camilla* Godman & Salvin, *chalciope* Hübner, *demophon* Linnaeus, *demophoon* Hübner, *licomedes* Cramer, *phaedra* Godman & Salvin, *meander* Cramer (Rydon 1971 included *chromus* Guérin-Méneville and *priene* Hewitson in his genus *Noreppe* and treated genera as tribes).

Authors: (1) Fruhstorfer (1915, 1916)\*; (2) Stichel (1939)\*; (3) Orfila (1950)\*; (4) Rydon (1971)\*; (5) Descimon et al. (1973-74)\*; (6) Papworth (1982)\*; (7) Johnson and Quinter (1982)\*. \* Emphasized certain characters, \*\* grouped taxa based on these characters.

February-April 1928, collector Kruger, sold by Niepelt 31 May 1928, in Biedermann Collection, Zurich, Switzerland (examined by second author); (6) Cisneros, Rio Dagua valley, 1000 m, 28 February 1928, collector Hopp, sold by Staudinger 15 May 1928, in Biedermann Collection (examined by second author); (7) Queremal, Colombia, November 1986, collector Julian Salazar, Manizales Museum (K. S. Brown Jr. pers. comm., sole South American deposition known to him); (8) Upper Rio Putumayo valley, 1981, local collectors, obtained by David Matusik (FMNH), deposited in American Museum of Natural History (AMNH) (Fig. 1D).

No specimens were located at Allyn Museum of Entomology (AME), British Museum (Natural History) (BMNH), Carnegie Museum of Natural History (CMNH), Field Museum of Natural History, Rijkmuseum van Natuurlijke Historie (Leiden, Netherlands) (RMNH), Museum National d'Histoire Naturelle (Paris), National Museum of Natural History (Smithsonian Institution).

**Variation.** Variation in the Chocó and Cauca samples appears slight (Fig. 1C), but the single Putumayo specimen (Fig. 1D) is distinctive, as follows: hindwing with emphatic medial band, area basad discal band with heavy blotched markings, three large submarginal eyespots (cells RS, M3, CuA1), and forewing with subapical stripe connected to postmedial stripe across vein M3.

**Biology.** The few acquirers of *P. werneri* provide the only sources of information about the butterfly's biology. Most specimens now in public (6) or private (3) collections derive from the pre-World War II era of highly financed butterfly sampling in the Neotropics. Initially, commercial interest prompted collection of *P. werneri* at several localities on the Pacific slopes of the Colombian Cordillera (mostly Chocó region). These sites proved extremely inhospitable (Hering & Hopp 1925), being rain forest with extraordinarily high precipitation; Gentry (1982) cites Chocó as the rainiest tropical forest in the world. Consequently, commercial interest in the insect waned, and only one specimen has since been recorded from the region (specimen 6 above). Specimens are so few that most private owners, to avoid deluges of buy offers, request anonymity.

**Biogeography.** Most specimens of *P. werneri* are from the Chocó region, though one (Queremal, Colombia) is near its eastern margin with the Cauca region. Very likely the extremely hydric Chocó region was a "forest refugium" during Pleistocene glaciations

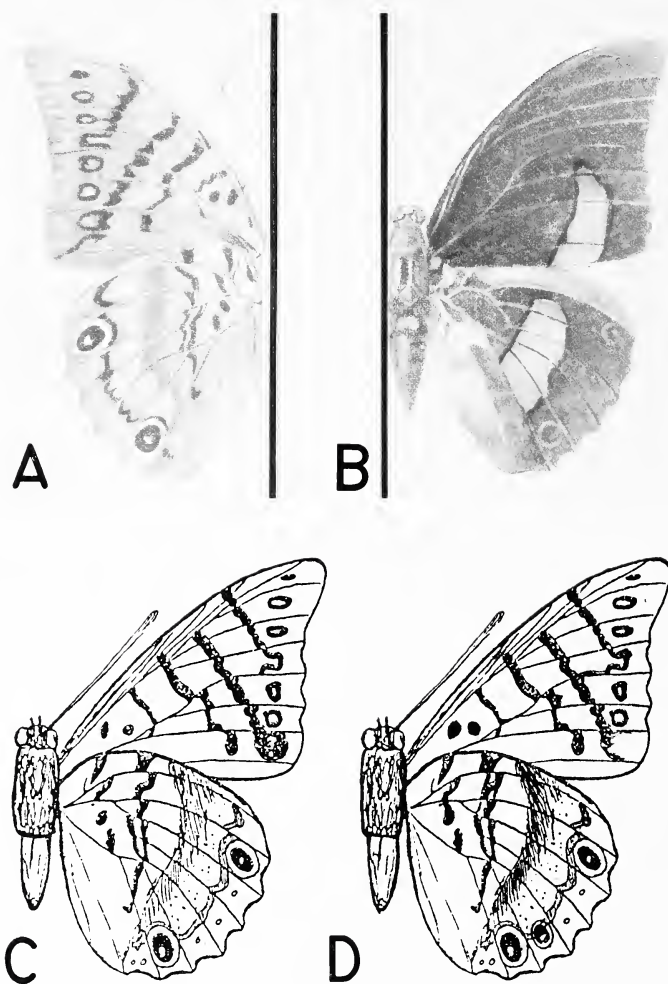


FIG. 1. *Prepona weneri*. A, B, Le Moult's (1932-33) figure of the holotype of *P. weneri*. A, Under surface. B, Upper surface. C, Reproduction of Hering and Hopp's (1925) original figure of holotype (showing distinctive markings characterizing Chocó and Cauca specimens). D, Drawing indicating distinctive markings on divergent specimen from upper Rio Putumayo region.

(Brown 1976, 1982), explaining the occurrence of a number of highly insular and seldom collected butterflies in it and immediately adjacent areas. Brown emphasizes the close geographic proximity of the Chocó and Cauca regions, and includes them in his "North-western Region" cluster (Brown 1976). He notes zones of hybridization between their taxa. If represented only by Chocó and Cauca specimens, *P. weneri* might be characterized as a seldom collected, insular cis-Andean species, typifying limited hydric habitat. However, a larger view of its taxonomy and biogeography is necessitated by specimen 8 above from the upper Putumayo region of south-central Colombia. This collection is



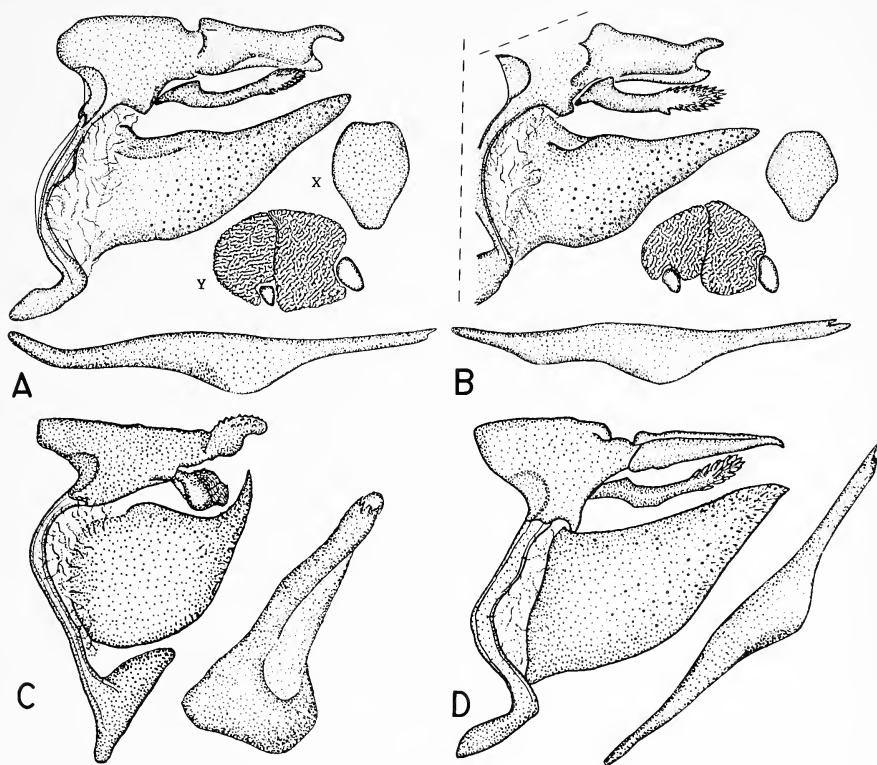


FIG. 2. Male genitalia of *Archaeoprepona* and *Prepona*, and male genitalia and abdominal androconia of *P. wernerii*. A, Topotypical *P. wernerii*, lateral view of genitalia with aedeagus removed (aedeagus, lateral view, beneath) and (x) ventral view, juxta, (y) lateral view, abdominal androconia at first and second abdominal spiracles. B, *P. wernerii* specimen from upper Rio Putumayo region (dashed lines indicating areas of genitalia not available for study because of prior damage to abdomen). C, *Archaeoprepona*, type species *demophon*, Rio de Janeiro, Brazil, same format except for x and y. D, *Prepona* type species *demodice*, Rio de Janeiro, Brazil, same format except for x and y. Females of *Archaeoprepona* and *Prepona* are illustrated in Orfila (1950).

particularly striking, since the Andes are usually considered as a very efficient barrier against faunal exchange. The Putumayo region is located disjunctly southwest of the Chocó and Cauca regions and included in Brown's (1976) "Andean Foothills" cluster. Brown notes very little hybridization between taxa of the Putumayo and Chocó-Cauca regions. Faunal elements of the Putumayo region are mostly trans-Andean. Thus, occurrence of *P. wernerii* in the Putumayo region appears biogeographically significant. It seems likely that disjunct distribution in *P. wernerii* is relict, reflecting former more widespread occurrence of perhumid biomes. Compared to the rest of the Andes, uplift of its northern elements was relatively recent (Gansser 1973). Consequent separation of *P. wernerii* into cis-Andean and trans-Andean nuclei associated with general climatic drying appears more likely than dispersal across the Andes in present or recent times. If further documented, the Putumayo *P. wernerii* could be construed as a subspecies.

## ACKNOWLEDGMENTS

Dale Jenkins (AME), K. S. Brown Jr. (Universidade Estadual de Campinas, Brazil) and two anonymous reviewers made helpful comments on the manuscript. We particularly thank David Matusik (FMNH) for obtaining the Putumayo specimen of *P. weneri* for AMNH, and A. M. Young (MPM) for providing a Chocó specimen for dissection. For location of additional material we thank David Matusik, H. J. Hannemann (ZMH), and three anonymous private collectors. The following also assisted in efforts to locate specimens: Philip Ackery (BMNH); L. D. Miller (AME); R. deJong (RMNH); J. E. Rawlins (CMNH); and K. S. Brown Jr (various South American inquiries). F. H. Rindge (AMNH) kindly facilitated assistance at AMNH including obtaining archival material. Robert Aronheim (Oakton, Virginia) generously provided an AMNH patron grant in 1981 for initial study of *Agrias* and *Prepona* butterflies which was subsequently followed by a similar grant from Joel B. Grae (Harrison, New York).

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## A NEW *EUPTYCHIA* SPECIES FROM NORTHWESTERN MEXICO (SATYRIDAE)

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**ABSTRACT.** A new euptychiine satyr, *Euptychia rubrofasciata*, is described based on 15 males and 4 females from NW Mexico, and compared with other similarly red-suffused species. A possible *Selaginella* foodplant association is discussed, and a mimetic assemblage involving satyrids is suggested.

**Additional key words:** Euptychiini, *Euptychia rubrofasciata*, mimicry, *Selaginella*.

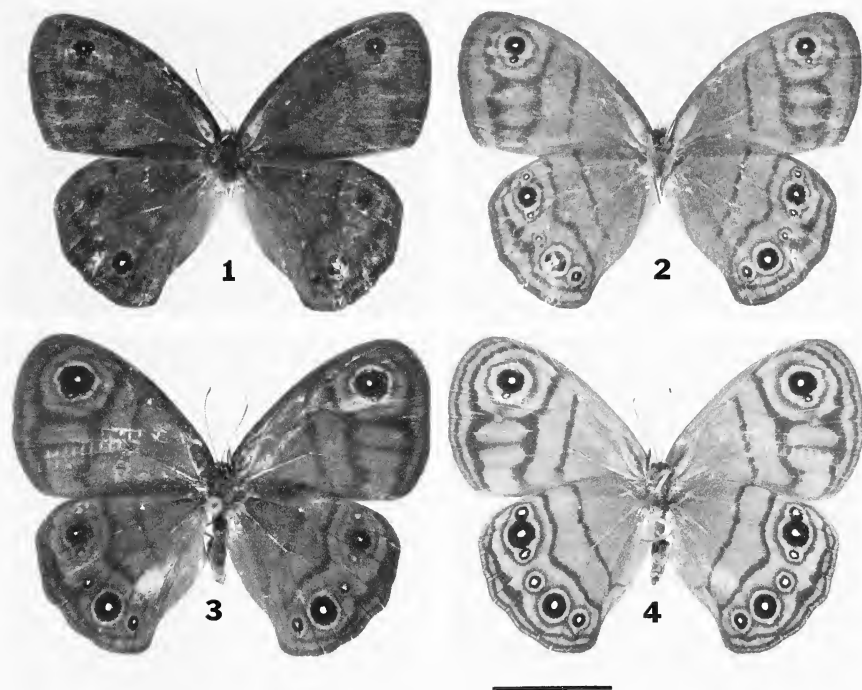
Mexican and northern Central American euptychiine Satyridae are unusual in that several species are strongly laved with red on the upper surface. This condition is shown in such diverse species as *Euptychia fetna* Butler, *Megisto rubricata* (W. H. Edwards), a few species of *Cyllopsis* (L. Miller 1974) and *Paramacera* (L. Miller 1972), *Cissia pellonia* (Godman & Salvin), and *C. cleophes* (Godman & Salvin). These red-patterned elements are rare in Euptychiini, and they are almost unknown in members of the tribe outside Mexico and northern Central America. Recently, Douglas Mullins showed us a series of a red-patterned species from Sonora, Mexico, that is totally unlike any other in this complex of "look alike". Later, James Brock and Jerry Powell sent additional specimens. This insect is the most ornate of the Mexican red-laved euptychiines, and is undescribed. A name for it is required for Brock and Mullins's forthcoming book on the butterflies of Sonora.

### *Euptychia rubrofasciata* L. & J. Miller, new species (Figs. 1-9)

**Male** (Figs. 1, 2). Head clothed with fuscous dorsal setae and somewhat paler hairs ventrad; area immediately behind eye narrowly white. Eyes rich brown, only slightly hirsute. Antennae plain brown above, light brown and narrowly ringed on shaft, dark brown beneath; tip black. Palpi clothed with long fuscous ventral setae and short lateral white hairs. Thorax and abdomen clothed with short fuscous dorsal and gray-brown ventral hairs. Legs clad with short gray-brown hairs.

Upper surface of forewing fuscous, grayer and paler distad of cell, with a darker fuscous submarginal shade and a single smooth, dark fuscous marginal line; wing laved with brick-red in posterior part of cell and just posteriad of cell, and with a darker red fascia from end of cell to middle of  $Cu_2-2A$ , a blackish fuscous subapical black ocellus in  $M_1-M_2$ , and a smaller one in  $M_2-M_3$ , each with a single silver pupil and narrow, dull ochereous ring. Upper surface of hindwing also fuscous, slightly paler subapically, with submarginal darker fuscous shade and a double dark fuscous marginal line. Wing laved with brick-red just outside and posteriad of cell, a red fascia outside cell from apex to near inner angle, blackish fuscous ocelli in  $Rs-M_1$  (large and diffuse),  $M_1-M_2$  (very small, almost a point and occasionally absent), and a well-defined, quite large ocellus in  $Cu_1-Cu_2$ , all ocelli consisting of a white pupil and a narrow, dull ochereous iris.

Under surface of forewing light gray-brown slightly shaded with red in and just posteriad of cell, with three brick-red fascia from near costa to inner margin, one across



FIGS. 1-4. *Euptychia rubrofasciata*. 1, 2, Holotype ♂, upper (1) and under (2) surfaces. 3, 4, Paratype ♀, upper (3) and under (4) surfaces. Scale line represents 10 mm.

cell, one just outside cell, and one beyond ocelli, the last two connected by brick-red streaks between veins from  $M_3$  to  $2A$ ; ocelli as on upper surface, but black with silver pupils and ochereous then fuscous rings surrounding both (not individual rings). Under surface of hindwing likewise gray-brown with three reddish fascia as described for forewing, and dark brown double marginal lines; six black ocelli with silver pupils and ochereous and fuscous rings from  $Sc+R_1$  to  $Cu_2-2A$ , the ones in  $Rs-M_1$  and  $Cu_1-Cu_2$  large and prominent, the one in  $Cu_2-2A$  of moderate size, the others quite small; ocelli in anterior three cells with rings coalesced.

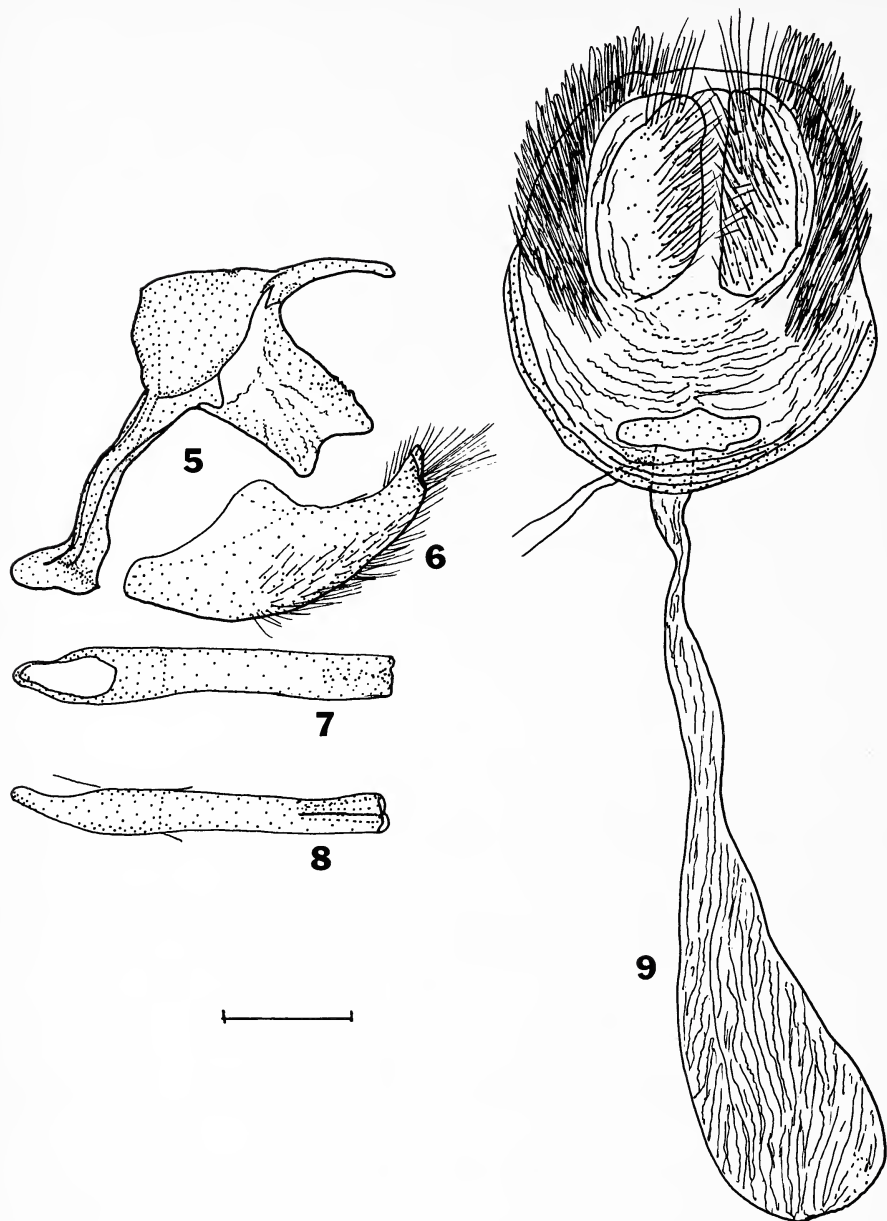
Forewing length of holotype ♂ 17.6 mm, of the 14 ♂ paratypes 17.3 to 19.2 mm, averaging 18.0 mm.

Male genitalia (Figs. 5-8) simple and lightly sclerotized; no superuncus as in most *Euptychia* (comparative illustrations in Forster 1964:81); uncus only slightly curved ventrad; brachia represented by only a very narrow sclerotized ring completely surrounding anus; valvae relatively unadorned, curved dorsad; penis short and straight with no obvious adornment.

**Female** (Figs. 3, 4). Head, thorax, abdomen, and appendages as in ♂, except thorax and abdomen below somewhat tanner.

Upper surface of forewing somewhat lighter than that of ♂ and more extensively laved with reddish fulvous, rusty fascia across cell and just beyond it, reddish streaks between veins from  $M_3$  to  $2A$ , a fuscous submarginal fascia and double marginal fuscous lines; blackish-brown coalesced ocelli with silver pupils in  $M_1-M_2$  (large and prominent) and  $M_2-M_3$  (very small) with coalesced narrow ochereous and fuscous rings. Hindwing above with similar ground color, red shading slightly more extensive than in ♂, and white-





FIGS. 5-9. Genitalia of *Euptychia rubrofasciata*. 5-8, Holotype ♂. 5, Uncus, tegumen, saccus, and associated structures, left lateral view. 6, Right valva, internal view. 7, Penis, dorsal view. 8, Left lateral view. 9, Paratype ♀, ventral view, genit. prep. M-7336-6 (J. Y. Miller). Scale line represents 0.5 mm.

pupilled fuscous ocelli in Rs-M<sub>1</sub> (large), M<sub>3</sub>-Cu<sub>1</sub> (very small, not present in all specimens), Cu<sub>1</sub>-Cu<sub>2</sub> (large), and Cu<sub>2</sub>-2A (small and absent in one specimen), each with ocherous and fuscous rings; red-brown submarginal fascia, two fuscous marginal lines.

Under surface of forewing somewhat less gray than in ♂ with similar markings except ocelli. Under surface of hindwing also less gray than in ♂, but marked similarly with larger ocelli and more prominent ocherous rings.

Forewing length of the 4 ♀ paratypes 17.6 to 20.0 mm, averaging 19.2 mm.

Female genitalia (Fig. 9) very lightly sclerotized with 8th segment heavily clothed in scales; papillae anales densely setose with 6–10 elongated setae posteriad; sterigma simple, lamella postvaginalis membranous with numerous folds, and lamella antevaginalis indicated by a lightly sclerotized plate; ductus bursae and corpus bursae membranous and strongly folded; attachment of ductus seminalis near atrium.

Described from 15 males and 4 females from the Sierra Madre Occidental of Sonora and Chihuahua, Mexico.

**Holotype** ♂ (Figs. 1, 2). MEXICO: Sonora, 13 mi (21 km) E El Novillo, 12 August [19]85 (J. P. Brock); ♂ genitalia preparation M-7341-v (Lee D. Miller).

**Paratypes.** All MEXICO: Sonora, 8 ♂, 1 ♀, same data as holotype, 1 ♀ (Figs. 3, 4), Rte. 16, 10 mi (16.1 km) E Trinidad, "Cypress" Canyon, 7 August [19]86 (D. D. Mullins); 2 ♂, 2 ♀, San Nicholas-Yecora Rd., 4.1–10.3 mi (5.6–16.5 km) E Santa Rosa, 7.viii.1986 (J. P. Brock) (1 with ♀ genitalia preparation M-7346-v (J. Y. Miller); 3 ♂, creek at 3000 ft (909 m), 6 mi (9.6 km) W Yecora, 31.vii.1984 (J. P. Brock); Chihuahua, [Sierra] Madre Occid[ental], Yepachic Rd., Canyon Rio Tomochic (oak/grass hillside), 31 July [19]84 (D. D. Mullins); Sinaloa, 1 ♂, 2 mi (3.2 km) SW Potrerillos, 4200' (1280 m) viii.7/8.[19]86 (J. Brown & J. Powell).

**Disposition of type-series.** Holotype ♂, 2 ♂ and 1 ♀ paratypes in Allyn Museum of Entomology; 1 ♂ paratype in collection of California Insect Survey; remaining 11 ♂ and 3 ♀ paratypes to be returned to J. P. Brock and D. D. Mullins for eventual distribution to other collections.

**Etymology.** The name refers to the unique brick-red fascia on both surfaces of all wings.

**Discussion.** That this insect proved to be a member of *Euptychia* came as a surprise. It is the largest known *Euptychia*, and superficially more closely resembles *Cissia*. However, the ♂ genitalia are unmistakably *Euptychia*, the abbreviated brachia fused with the tegumen. The ♀ genitalia are simple and very lightly sclerotized, this also in keeping with the apomorphic condition for *Euptychia*.

The only published life history information about *Euptychia sensu lato* is that by Singer et al. (1971) who found the white congener, *E. westwoodi*, feeding as a larva on the lycopsid *Selaginella*. Those authors suggested that *Selaginella* might have "rather potent biochemical defenses," since few herbivores attack them, and that these defenses might convey some protection to *Euptychia*. These toxic chemical defenses have yet to be proven (J. Beckner pers. comm.), but seem reasonable. The Mexican *E. fetna* feeds also on *Selaginella* (J. Llorente and others pers. comm.). *Euptychia westwoodi* appears to be in a mimetic complex involving lycaenids and riadinids (Singer et al. 1971:1342).

We suggest that *E. rubrofasciata* also feeds as a larva on *Selaginella*. This is supported by Brock (pers. comm.), who writes "... nearly all the *Euptychia* were found on a shady [canyon] wall loaded with a *Selaginella* species." He further mentioned that he identified the *Selaginella* because it was so abundant and conspicuous at the spot where the new species was most abundant. Mullins (pers. comm.) independently confirms this habitat preference.

Assuming the above foodplant and its toxicity to predators, the present new species and *E. fetna* may be Muellerian mimics, and the other red-laved euptychiines (and perhaps other butterflies) could be Batesian mimics of them.

#### ACKNOWLEDGMENTS

We thank D. D. Mullins for sending the first specimens of this insect for description, and J. P. Brock and J. A. Powell for additional ones. Thanks are due J. Llorente for

discussions concerning *E. fetna* and to J. Beckner for discussions about the properties of *Selaginella*.

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## A NEW SPECIES OF *ETHMIA* FROM THE FLORIDA KEYS (OECOPHORIDAE: ETHMIINAE)

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**ABSTRACT.** *Ethmia powelli* is described from Upper Matecumbe Key based on 123 specimens. It is related to *E. humilis* Powell and *E. julia* Powell, in the *confusella* species-group, by genitalic characters, and is distinguished from *E. farrella* Powell by the small wingspan and fewer forewing black spots.

**Additional key words:** *Ethmia powelli*, *E. farrella*.

The genus *Ethmia* was monographed for the known New World fauna by Powell (1973). In Florida seven species are now recorded (Florida Lepidoptera Survey), mostly being Caribbean elements present in southern Florida. The new species was collected after the publication of Powell's (1973) monograph and is described here to make the name available for a revision of Kimball (1965). Description of the species has awaited collection of more specimens, but only recently has one additional individual been collected. Capuse (1981) reviewed the Cuban ethmiines but did not include the species described from Florida. Specimens are deposited with the Florida State Collection of Arthropods (FSCA) and my own collection (JBH), with paratypes distributed to the University of California, Berkeley (UCB), and the National Museum of Natural History, Washington, D.C. (USNM).

### *Ethmia powelli* Heppner, new species (Figs. 1-4)

Forewing length 4.0-4.7 mm (N = 100) (male); 4.1-4.9 mm (N = 23) (female).

**Male** (Fig. 1). **Head.** Silvery gray-white with black central mark on vertex; labial palpus silvery gray-white with lateral black mark on each segment and black laterally near base. **Thorax.** Silvery white; legs white, with fore- and mid-tibiae and tarsi marked with black; hind legs white. **Forewing.** Ground color silvery white with numerous black spots (costal spots at base and  $\frac{1}{8}$  from base; cubital area with elongated spots near base and at hindwing, with a small round spot near dorsal margin; a large elongate spot mid-wing and another along tornus); terminal black spots extending along costa on apical  $\frac{1}{4}$ ; fringe silvery; venter silvery gray. **Hindwing.** Unicolorous pale gray with dark gray at margin; fringe gray; venter similar. **Abdomen.** Silvery white with darker gray dorsum. **Genitalia** (Fig. 3). Tegumen with slightly bulbous terminal points; vinculum rounded, without saccus; valva subquadrate with prolonged distal end having 3 large spines and 2 smaller truncated central spines, with a large curved hooklike process on dorsal margin near apex; anellus an elongated tube (troughlike), dorsally open; aedeagus similar to that of *E. humilis*, with bulbous phallobase; cornutus indistinct.

**Female** (Fig. 2). Similar to male; forewing terminal black spots slightly larger on average than in male. **Genitalia** (Fig. 4). Setose ovipositor; posterior apophyses  $3\times$  length of anterior apophyses; sterigma composed of fused anterior apophyses extensions; ductus



FIGS. 1, 2. *Ethmia powelli* paratypes, Islamorada, Monroe Co., Florida. 1, Male, 2, Female.

bursae with sclerotized collar at ostium, then spiralled to ovate corpus bursae; signum a small sclerotized depression.

**Type material.** Holotype: male, 1 mi [1.6 km] SW Islamorada, Upper Matecumbe Key, 23-VI-1974, J. B. Heppner (slide JBH 1773) (FSCA). Paratypes: 99 males, 23 females, same data as holotype. Paratypes distributed to FSCA, UCB, USNM, and author's personal collection. Additional specimen: Key Largo, Monroe Co., 30-VIII-1986 (1 male), L. C. Dow (FSCA).

**Hosts.** Unknown. One species in the *confusella* species-group feeds on *Bourreria ovata* (Boraginaceae).

**Remarks.** Thus far, *Ethmia powelli* has been collected only twice in the Florida Keys. There are no records of it from any Neotropical locality; thus, the species may be native to Florida. Relations of *E. powelli* by some genital characters appear nearest to *E. humilis*

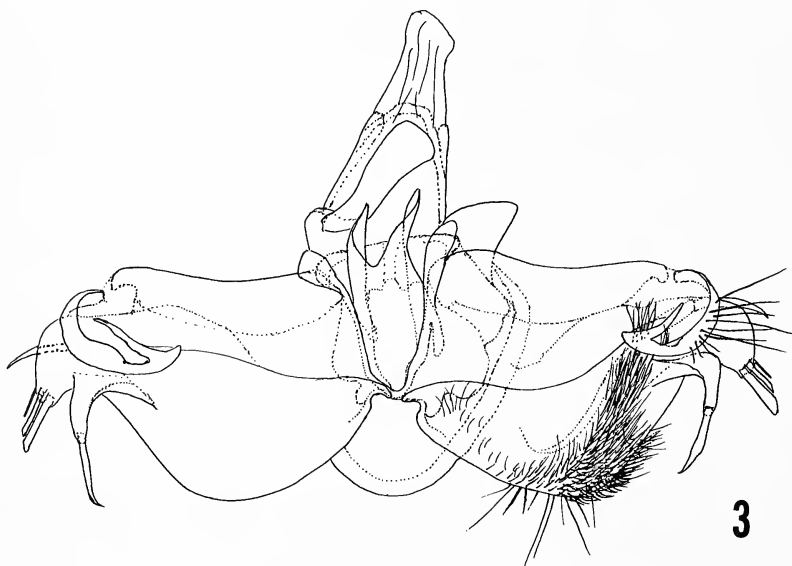


FIG. 3. *Ethmia powelli* male genitalia, aedeagus omitted (JBH 1773).





FIG. 4. *Ethmia powelli* female genitalia (JBH 1774).

Powell and *E. julia* Powell in the *confusella* species-group. This is a primarily tropical group with several species also occurring in S Florida (includes records of West Indian species recently found in the Florida Keys). Forewing maculation, however, is more similar to *E. farrella* Powell. In the key to species in Powell (1973), *E. powelli* keys to couplet 118, differing from *E. farrella* in having fewer black spots on the forewings, and in being significantly smaller, 4.0–4.9 mm versus 6.5–7.0 mm for *E. farrella*. The male genitalia are particularly diagnostic, having 5 spines on the distal end of the valva, and the central 3 of these being truncated; *E. humilis* has only 3 curved spines on the valva, likewise for *E. julia*. Female genitalia are not very similar to the other species; the sterigma is most similar only to the Central and South American *Ethmia catapeltica* Meyrick. The female ductus bursae in *E. humilis* is not coiled as in most *Ethmia* species and the sterigma is very different in *E. farrella*.

*Ethmia powelli* appears to be one of the smallest species in *Ethmia*. The species is named in honor of Professor J. A. Powell, University of California, Berkeley.

#### ACKNOWLEDGMENTS

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## LARVAE OF NORTH AMERICAN *LEUCONYCTA* (NOCTUIDAE)

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**ABSTRACT.** Mature larvae of *Leuconycta diptheroides* (Guenée) and *L. lepidula* (Grote), the only known members of *Leuconycta*, are illustrated, described, and diagnosed based on eight specimens of the former reared from ova on *Solidago* sp. and two specimens of the latter reared from ova on *Taraxacum* sp. Although resembling one another in coloration and structure, larvae of the two species can be distinguished by characters in the hypopharyngeal complex.

**Additional key words:** Acontiinae, *Leuconycta diptheroides*, *L. lepidula*, hypopharyngeal complex.

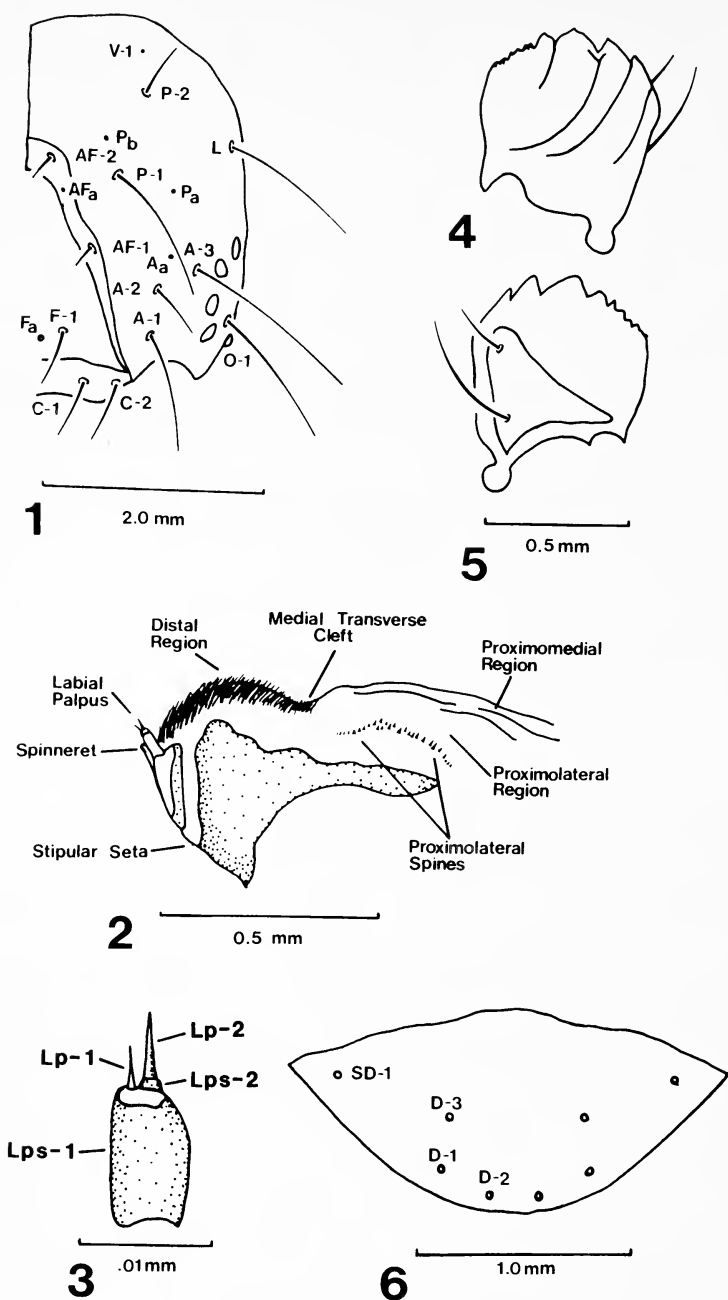
The North American noctuid genus *Leuconycta* Hampson (Acontiinae) contains two species, *L. diptheroides* (Guenée) and *L. lepidula* (Grote). Larval systematic and life history information has been presented by Dyar (1898), Forbes (1954), and Crumb (1956). Crumb was unable to find color or structural differences by which to separate larvae of the species of *Leuconycta*. The purpose of this paper is to more fully describe and diagnose mature larvae, especially with respect to mouthparts and chaetotaxy, which have been shown by Godfrey (1972) to be of taxonomic value.

*Leuconycta diptheroides* and *L. lepidula* are common and widely distributed in North America, both ranging from Nova Scotia S to North Carolina, and W to Manitoba, Kansas, and Colorado (Forbes 1954). Larvae of *L. diptheroides* have been recorded feeding on *Solidago* sp. (Dyar 1898), and those of *L. lepidula* on *Taraxacum* sp. (Forbes 1954).

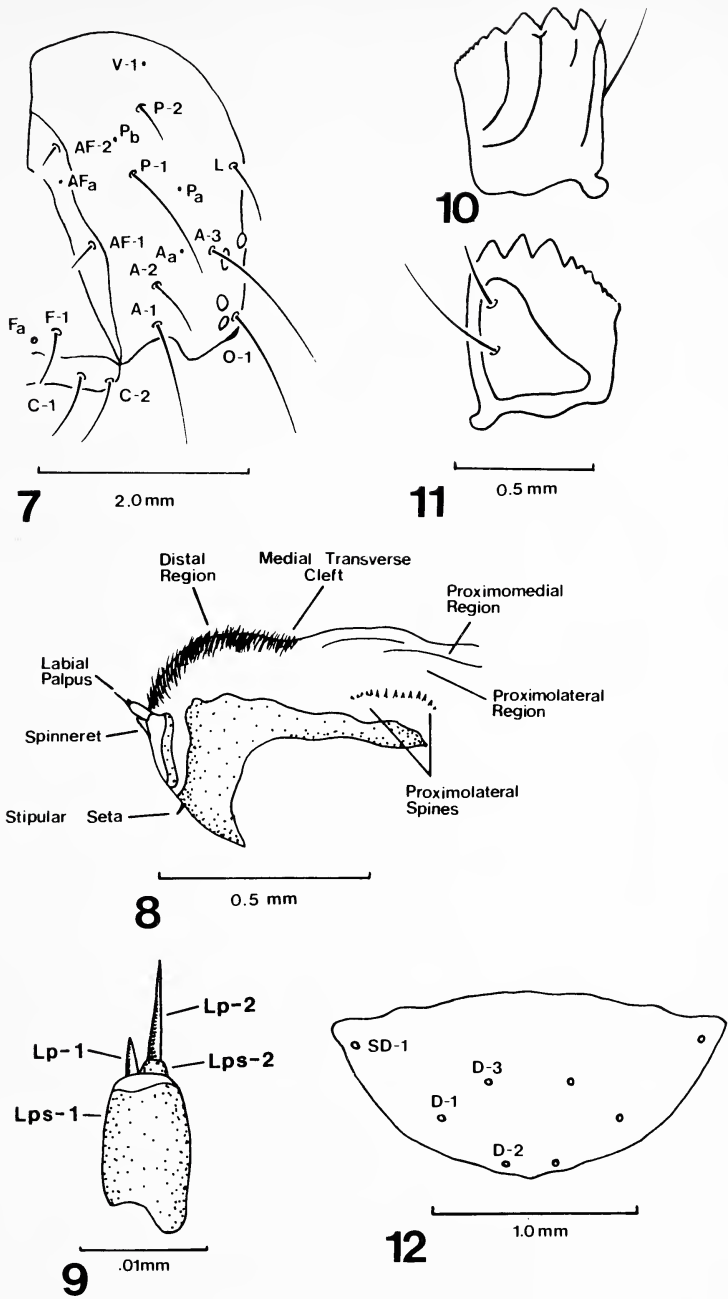
Terminology and abbreviations here follow Godfrey (1972). Specific collecting localities and dates are provided in individual descriptions.

### Genus *Leuconycta* Hampson (Figs. 1-14)

**Diagnostic description** (diagnostic characters in *italic*). Head 1.6-2.5 mm wide, total body length 25.8-32.2 mm (N = 10). *Head and body smooth. Body broad at middle, tapering slightly anteriorly and posteriorly. Prolegs present on abdominal segments (Ab) 3-6, size increasing posteriorly; those of Ab6 twice size of those on Ab3. Crochets uniordinal. All setae simple. Coloration of living material.* Head green, no lines or markings present. Body green, darker at edges of mid-dorsal and subdorsal lines and ventral edge of subdorsal area; ventral area lighter green; mid-dorsal and subdorsal lines white, the latter wider and more irregular; spiracular line greenish white, more whitish on dorsal and ventral edges and bordered dorsally by a narrow red line on thoracic segments (T)1 and 2. Cervical and anal shields concolorous with trunk, the latter with a white medial and two white lateral lines. Pinacula white, the dorsal pinacula larger than lateral and ventral pinacula. Spiracles yellow with black peritremes. True legs greenish, slightly brown distally. Proleg shields concolorous with trunk. **Coloration of preserved material.** Head and body light cream color. Lines and pinacula concolorous with body.



FIGS. 1-6. *Leuconycta diptheroides* larval structures. 1, Head, frontal view. 2, Hypopharyngeal complex, left lateral view. 3, Labial palpus, lateral view. 4, Left mandible, oral surface. 5, Left mandible, outer surface. 6, Anal shield, dorsal view.



FIGS. 7-12. *Leuconycta lepidula* larval structures. 7, Head, frontal view. 8, Hypopharyngeal complex, left lateral view. 9, Labial palp, lateral view. 10, Left mandible, anal surface. 11, Left mandible, outer surface. 12, Anal shield, dorsal view.



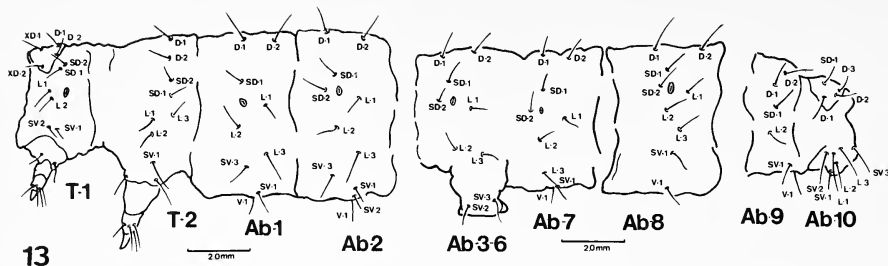


FIG. 13. *Leuconycta diptheroides*. Dorsal and lateral chaetotaxy of prothoracic (T1), mesothoracic (T2), and abdominal segments (Ab1-3, Ab6-10).

Spiracles white, peritremes dark brown. **Head** (Figs. 1, 7). Cervical indentation shallow; adfrontal sutures terminating at epicranial suture; epicranial suture longer than height of frons; frons slightly higher than its basal width. Adfrontal setae (AF)2 above, and posterior head setae (P)1 below, even with, or slightly above apex of frons; anterior head puncture (Aa) below a straight line between posterior head puncture (Pa) and anterior head setae (A)3. P2, P1, and AF1 in a straight line, Aa closer to A3 than to A2, A1-A3 forming an obtuse angle at A2; lateral head seta (L) even with or slightly below juncture of adfrontal ecdysial lines. Distance between ocelli (Oc)2-Oc3 greater than Oc1-Oc2 and Oc3-Oc4. **Mouthparts.** Hypopharyngeal complex (Figs. 2, 8): *Spinneret short and broad. Stipular setae varying from extremely short to slightly less than 1/4 length of 1st segment of labial palpus (Lps1).* Labial palpi (Figs. 3, 9) with length of segments variable. Distal and proximal regions of hypopharyngeal complex separated by shallow medial transverse cleft; distal region of hypopharyngeal complex covered with spines which are long, slender, shorter proximally; proximolateral region with spines small, triangular, numbers variable. **Mandible** (Figs. 4, 5, 10, 11). Two well separated outer setae present; inner surface with 3 distinct ridges, the last short; outer margin with 12 teeth, the 1st small, 2nd to 4th well developed and angular, 5th to 12th small and angular.

**Thorax.** Prothoracic segment (T1) (Figs. 13, 14): Shield smooth and weakly sclerotized, subdorsal body setae (SD)1 and 2 separated from prothoracic shield, setae SD1 and lateral body seta (L)2 fine, hairlike, and with a thickened sclerotized annulus at base; major axis of prothoracic shield passing behind SD1 and SD2, and between subventral body setae (SV)1 and 2; spiracle broadly elliptical, height less than twice its width. **T2-3** (Figs. 13, 14): SD1 fine, hairlike, with a thickened sclerotized annulus at base. Tarsal claws with basal angles acute. Metathoracic coxae contiguous. **Abdomen.** Dorsal and lateral chaetotaxy of Ab2-6 with 3 SV setae; SV1 and SV2 setal insertions well separated. Ab7-8 with 1 SV seta. Ab9: SD1 fine, hairlike, with a thickened annulus at base. Ab10: Anal shield as in Figs. 6 and 12. Dorsal margin convex, posterior margin entire; subanal setae widely separated.

### *Leuconycta diptheroides* (Guenée) (Figs. 1-6, 13)

Head 2.2-2.5 mm wide, total length 25.8-31.0 mm (N = 8). Larva as described above except: Hypopharyngeal complex (Fig. 2) with spinneret about 1/2 length of 1st segment of labial palpus (Lps). Labial palpus (Fig. 3) with Lps1 about 3 times length of seta borne by 1st segment of labial palpus (Lp), 13 times length of Lps2, 2 times length of Lp2. Lps2 less than 1/4 length of Lp1. Stipular setae very short, about 1/4 length of Lps1, less than 1/4 length of Lp1, subequal to Lps2. Proximolateral spines small, 10-14 small triangular spines.

**Material examined.** 8 specimens: New Minas, Kings Co., Nova Scotia, reared on *Solidago* sp. from ova obtained from a female collected 19 June 1985. Moth collected,

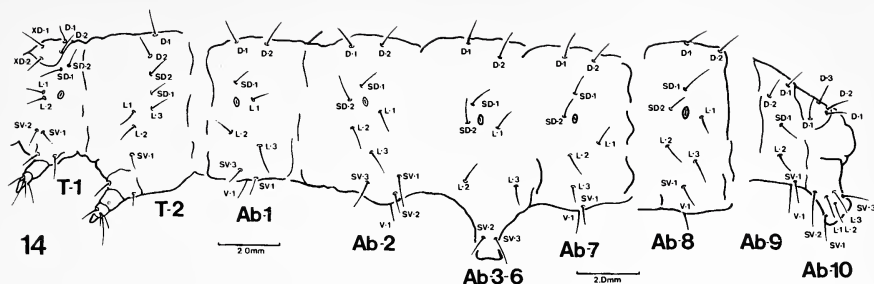


FIG. 14. *Leuconycta lepidula*. Dorsal and lateral chaetotaxy of prothoracic (T1), mesothoracic (T2), and abdominal segments (Ab1-3, Ab6-10).

determined, and larvae reared by author. All specimens in Nova Scotia Museum collection, Halifax, Nova Scotia.

### *Leuconycta lepidula* (Grote) (Figs. 7, 12, 14)

Head 1.6–1.8 mm wide, total length 31.3–32.2 mm (N = 2). As described for genus except: Hypopharyngeal complex (Fig. 8) with spinneret slightly less than  $\frac{1}{2}$  length of Lps1; labial palpus (Fig. 9) with Lps1 slightly less than 5 times length of Lp1, 12 times length of Lps2, less than 2 times length of Lp2. Lps2 about  $\frac{1}{2}$  length of Lp1. Stipular seta slightly less than  $\frac{1}{5}$  length of Lps1, longer than Lp1, and about twice length of Lps2; proximolateral region with 10–14 triangular spines; spines larger than in *L. diptheroides*.

**Material examined.** 2 specimens: Chicago, Illinois, reared on *Taraxacum* sp., 24 June 1934, A. K. Wyatt. Specimens in U.S. National Museum, Washington, D.C.

### Discussion

Larvae of *L. diptheroides* and *L. lepidula* resemble one another closely, but can be separated by the following mouthpart characters: In *L. diptheroides*, the stipular seta is  $\frac{1}{15}$  the length of Lps1 compared with *L. lepidula* in which this seta is slightly less than  $\frac{1}{5}$  length of Lps1, and proximolateral spines are larger in *L. lepidula* than in *L. diptheroides*.

Franclemont and Todd (1983) placed *Leuconycta* in Acontiinae, whereas Forbes (1954) and Crumb (1956) placed it in Amphipyrinae. The latter two authors considered larval characters; those such as the open silk pore on the spinneret, presence of five pairs of abdominal prolegs and two SV setae on Ab1 strongly indicate Amphipyrinae, but resolution of the discrepancy should be based on a wider range of material than examined here.

### ACKNOWLEDGMENTS

I thank D. C. Ferguson, Systematic Entomology Laboratory, U.S. National Museum, Washington, D.C., for supplying specimens of *L. lepidula*, and Arthur Lightfoot of Agriculture Canada, Kentville, Nova Scotia, for photographing the plates.

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## GENERAL NOTES

### NEW DISTRIBUTION RECORDS AND A PROBABLE NEW LARVAL HOST PLANT FOR *PHILOTES SONORENSIS* (LYCAENIDAE) IN KERN AND TULARE COUNTIES, CALIFORNIA

**Additional key words:** Sierra Nevada, *Dudleya calycicola*, Crassulaceae.

*Philotes sonorensis* (Felder & Felder) is of limited distribution, known only from Sierra Co. in north-central California S to Cedros Island, Baja California Norte, Mexico (John W. Brown pers. comm.). Published distribution records do not include Kern and Tulare counties, California (Langston, R. L. 1963, J. Lepid. Soc. 17:201-223; 1965, J. Lepid. Soc. 19:95-102; 1969, J. Lepid. Soc. 23:49-62; Shields, O. 1973, Bull. Allyn Mus. 15:1-16; Shapiro, A. M. 1974, Pan-Pac. Entomol. 50:442-443). Recently, *P. sonorensis* was discovered at scattered locations in these two counties and in the southern Sierra Nevada. New distribution records (Fig. 1) are as follows:

Kern Co.: Pleito Creek and Canyon (located nr. Mt. Pinos at S end of San Joaquin Valley), 1 ♂, 16 IV 81 (W. D. Patterson). Laura Peak ("Rock Tip" on some maps) in Piute Mts. E of Lake Isabella; adults found by author in canyon on S slope nr. rocky outcrops at 3600-4600 ft (1097-1402 m) elev. on this peak of 5260 ft. (1603 m), 2 ♂, 28 III 87; 3

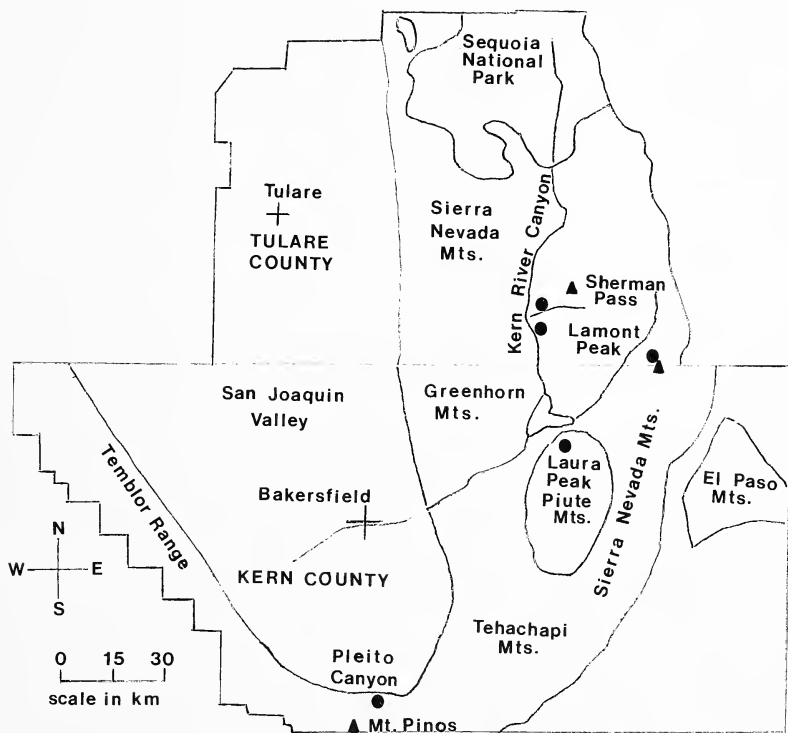


FIG. 1. Map of Kern and Tulare counties, California, showing new localities for *Philotes sonorensis* (black dots). Triangles represent nearby mountain peaks important as reference points. Cross marks represent major cities.

♂, 29 III 87, 2 ♂, 14 IV 87. The latter locality is dry grassland with some junipers on steep rocky slopes. The dry streambed probably carries water for short periods following rainfall.

Tulare Co.: Canyon 1.6 km N of Lamont Peak S of Chimney Peak Road, 3 ♂, 10 IV 85 (K. Davenport). Canyon N of Sherman Pass Road 5.6 km E of Kern Canyon Road, 5 ♂, 2 IV 87 (Davenport); 1 ♂, 5 IV 87 (R. Meyer); 2 ♂, 1 ♀, 14 IV 87 (Davenport & K. Richers). Kern River Canyon 1 km N of Roads End at dam, in side canyon E of road, 4 ♂, 1 ♀, 2 IV 87 (Davenport); 1 ♂, 1 ♀, 5 IV 87 (Meyer); 2 ♂, 14 IV 87 (Davenport & Richers), 8 ♂, 1 ♀, 9 III 88 (Davenport).

The Tulare Co. colonies are in rocky canyons of limestone or granitic composition with small streams between 3000 and 5000 ft (914–1524 m) elev., in chaparral and foothill woodland.

The host plant of *P. sonorensis* in the southern Sierra Nevada (including Laura Peak in the Piute subrange) is likely *Dudleya calycicola* Bartel & Shevock (Crassulaceae), which occurs locally "on pre-Cretaceous limestones within chaparral or pinyon-juniper woodland at 850–1700 m" (Bartel, J. A. & J. R. Shevock 1983, *Madroño*, 30:210–216), and is limited in distribution to Kern, Tulare, and extreme SW Inyo counties (J. A. Bartel pers. comm.). Adults are closely associated with *calycicola* (no other *Dudleya* spp. present) at the new localities. All known hosts are in the genus *Dudleya* (Shields, O. 1973, *Bull. Allyn Mus.* 15:9–11). Collections and identifications of *Dudleya* at the new localities were made by J. F. Emmel, J. A. Bartel, and J. R. Shevock. No larvae were collected or reared, and oviposition was not observed. The discovery of *Philotes sonorensis* on Laura Peak was made using herbarium records of *Dudleya calycicola* provided by Emmel.

Eight voucher specimens of *Philotes sonorensis* representing each of the four new Sierran localities have been deposited in the Natural History Museum of Los Angeles County, Los Angeles, California. Remaining specimens are in private collections.

I thank J. A. Bartel, J. W. Brown, J. F. Emmel, R. Meyer, K. Richers, J. R. Shevock, O. Shields, and W. D. Patterson for records and assistance.

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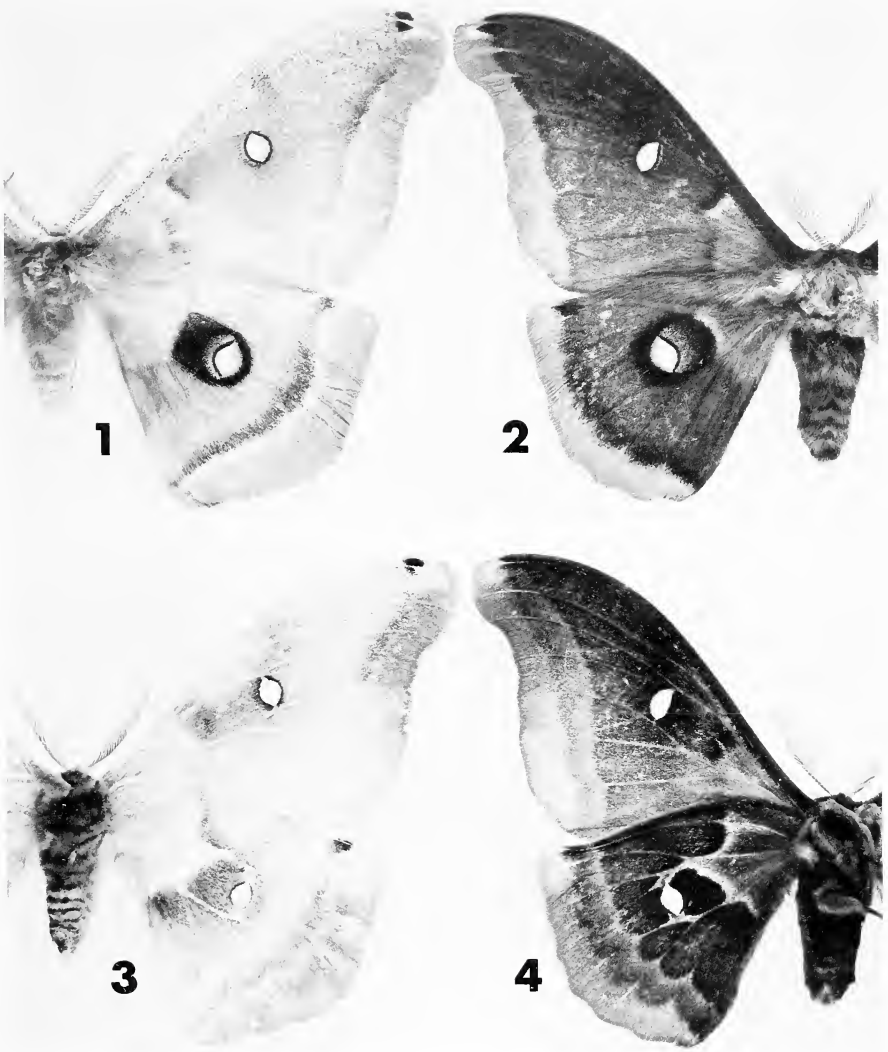
#### A MELANIC MALE OF *ANTHERAEA POLYPHEMUS POLYPHEMUS* (SATURNIIDAE)

**Additional key words:** Canada, New Brunswick, light trap.

W. B. Preston and W. B. McKillop (1979, *J. Lepid. Soc.* 33:147–148) summarized the known information about melanic *Antheraea polyphemus polyphemus* (Cramer), and published the first illustration of a melanic specimen. Our specimen appears to be the fourth ever collected.

On the night of 30 June–1 July 1986, we collected a melanic male of *A. p. polyphemus* on a white sheet illuminated by a 250-W M-V bulb, at the edge of a sphagnum bog in the Acadia Forest Experiment Station, 20 km E of Fredericton, New Brunswick. Dorsally, this male (Fig. 2) differs from typical *A. p. polyphemus* (Fig. 1) by having a dark chocolate ground color. Prothorax and costal edge of upper forewings are black so that the apical and subapical forewing spots are not discernible as distinct spots. However, the grayish lilac dash from the subapical spot toward the forewing apex is still present. In typical specimens, prothorax and costal edge are whitish gray. The blackish component of the submarginal band on fore- and hindwings is exaggerated, obliterating the pinkish shading beyond it on the hindwings but leaving it just discernible on the lower half of the forewings.





FIGS. 1-4. Males of *Antheraea polyphemus polyphemus* (Cramer) from New Brunswick. 1, Typical dorsum. 2, Melanic dorsum. 3, Typical venter. 4, Melanic venter.

The discal spots on both fore- and hindwings are typical, with the transparent center surrounded by an ocher-yellow ring, edged outwardly with a black ring. The whitish-blue semicircle that outwardly edges the black ring on the proximal side is still discernible on the forewing and very extensive on the hindwing. The black component of the hindwing submarginal band is conspicuously recurved along the outer margin of the wing. The outer margin of both wings beyond the submarginal band is of the usual bright ocherous tawny brown, giving the specimen a distinctive bicolored appearance.

On the underside, the wings are uniformly dark chocolate (Fig. 4), and the markings

contrast less than those of a typical specimen (Fig. 3). Costal regions of both fore- and hindwings are dark, as is the basal area of both wings.

The specimen is in the senior author's private collection.

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## BOOK REVIEWS

THE MONARCH BUTTERFLY: INTERNATIONAL TRAVELER, by Fred A. Urquhart. 1987. xxii + 232 pp., 24 pp. color photographs. Nelson-Hall, Chicago. Hard cover. \$31.95.

To his everlasting credit Fred A. Urquhart showed that the monarch butterfly migrates from Canada to overwintering sites in Mexico. In his most recent book Urquhart gives an enlightening account of his pioneering investigations of North America's most famous butterfly, including its morphology, development, behavior and ecology.

Urquhart documents the migration of the monarch butterfly in historical and personal terms. He writes in the first person and selects information intended for a popular audience. The result is informative and exciting. He describes how he developed the tagging technique for following monarchs. He reveals the clues that ultimately led to the discovery of the Mexican overwintering sites. His conversational, informal style allows him to include anecdotal digressions that enrich the factual account.

Often when writing about the biology of the butterfly, Urquhart poses a simple question and then describes an experiment which he conducted looking for answers. What determines which trees monarch butterflies choose for roosting? Do pheromones help monarch butterflies aggregate? How does a monarch caterpillar which has fallen off a milkweed plant find its way back to that plant or another? The question-and-experiment format generates a certain suspense and captures the reader's attention. The experiments are intriguing even when inconclusive.

Few entomological authors dare to write about the emotions which their love of insects arouses. Scientific papers require a tone of objectivity, and expressions of pleasure come as a surprise. In this book Urquhart overcomes the inhibitions which desiccate more scholarly treatises. Urquhart understands that his audience wants to know why a person would go to the extremes he did in pursuit of a common butterfly (p. 153):

Those who have had a dream and have lived to see that dream come true will have some conception of my feelings when I first entered the Mexican forest and there, before my eyes, was the realization of a dream that had haunted me since I was a lad of sixteen.

On the negative side, Urquhart's personal approach overemphasizes his own work at the expense of others. For example, in the opening chapter about the monarch butterfly's foodplant, he ignores the ecological chemistry of milkweeds. Later he alludes to the transfer of milkweed toxins to monarch butterflies, but only to dismiss its importance.

Urquhart's failure to recognize the work of others leads him to farfetched speculation. His attempt to explain control of sexual maturation of migrants is an example (p. 121):

As our small planet earth travels in its elliptical orbit around the sun, it is possible that twice each year it passes through an area rich in some sort of radiation that impinges upon animal life. The radiation cycle might affect in some manner the cells of the body, causing reproductive organs to abort in the fall and develop in the spring and to initiate the migratory response. Perhaps our astronomy researchers may add a missing part to the migration puzzle. Perhaps animal life on our earth is being controlled by what is happening in outer space more than we now consider feasible. . . .

Urquhart could have avoided this fantasy if he had discussed hormonal control of monarch butterfly development, and photoperiodic regulation of the timing of this development (reviewed in Rankin, M. A., M. L. McAnelly & J. E. Bodenhamer 1986, The oogenesis-flight syndrome revisited, pp. 27-28 in Danthanarayana, W. (ed.), *Insect flight: Dispersal and migration*, Springer-Verlag, Berlin, 289 pp.).

Urquhart makes generalizations that violate basic biological principles. He writes (p. 194): "The characteristics of size, shape and color that we now see in different species of butterflies were indelibly fixed in the hereditary gene complex millions of years ago and have persisted to the present time." It is doubtful whether any trait can be "indelibly

fixed," since genes are neither indelible nor fixed. Urquhart implies that evolution of butterfly coloration eons ago stopped. The fossil record does not answer the question, but industrial melanism demonstrates that, at least for some Lepidoptera, such evolution continues. When Urquhart does address the literature, he becomes polemical (p. 190):

The scientific literature abounds with attempts to justify the mimicry theory as it applies to birds feeding on butterflies. These papers contain an impressive array of tables, charts and graphs resulting from experiments carried out in the crowded confines of cages in a laboratory. By the use of abstruse terminology the research assumes an aura of highly qualified investigations, but, when carefully analyzed, contains nothing of real value and no meaningful conclusions.

Much of the information Urquhart presents may be found in his earlier book (Urquhart, F. A. 1960, *The monarch butterfly*, Univ. Toronto Press, Canada, 361 pp.). That work contains an extensive bibliography, which the current book lacks. More recent findings are described in Urquhart's other publications, which he lists in his current book.

Fred A. Urquhart made perhaps the most spectacular discovery in the field of lepidopterozoology this century. This book will interest anyone who wonders what he has to say about monarch butterflies and his studies of them. However, to find out what others have to report about this species, readers will have to consult sources other than Urquhart's book.

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THE GEOMETROID MOTHS OF NORTH EUROPE (LEPIDOPTERA: DREPANIDAE AND GEOMETRIDAE), by Peder Skou. Translated from Danish edition by Elisabeth Folino. Entomograph Vol. 6. 1986. 348 pp., 24 color pls., 358 figs. E. J. Brill/Scandinavian Science Press, Leiden & Copenhagen. 17 × 25 cm, hard cover. \$100.00.

This book covers all moths of the families Drepanidae, Thyatiridae, and Geometridae known from Norway, Denmark, Sweden, and Finland. After a brief section introducing categories of information to follow, the author moves directly to species treatments. These consist of scientific name, author and year citation, plate and figure references, description, range, habitat, flight period, and biology. Descriptions are usually brief, with emphasis on variation. The color plates are among the best I have seen in sharpness and color value, comparing favorably with those in Skinner's 1984 *Moths of the British Isles*. Color plates include both sexes and sometimes additional varieties; they accomplish well the identification of most species. Genitalia drawings for some species are included, especially in difficult genera such as *Eupithecia*. Similar species are discussed when separation is difficult, and the author has added text figures showing useful body parts such as wing patterns, heads, and abdomens, with arrows pinpointing diagnostic features.

The worldwide range for each species is given, followed by detailed locality information for the four countries featured. The habitat section gives variably detailed characteristics of known sites, with black-and-white photos of typical habitats for many species. Flight periods are general ("From late April until mid-May."), and the biology section features larval foodplants, time of year in larval stage, place of pupation, and other information. Larvae and pupae are not described, but the book is generously illustrated with large black-and-white photos of the caterpillars, usually on their foodplants. A final line tells how the adult is best collected (at light, usually).

Following the species treatments are a selected bibliography and a table of distribution for all species in the four northern countries.

The arrangement of taxa anticipates a new catalogue of European moths in preparation by K. Schnack. Thus Thyatiridae are treated as a subfamily of Drepanidae. The subfamilies of Geometridae are named as we now recognize them in the North American fauna, but

they are arranged in the same order as in the McDunnough 1938 *Check List*: Archiearinae, Oenochrominae, Geometrinae, Sterrhinae, Larentiinae, and Ennominae. The Hodges et al. 1983 *Check List* is the same except that Ennominae are moved to a position between Oenochrominae and Geometrinae.

This book builds on several previous works, and appears to be an excellent identification guide for species. Taxa above species are not described or defined, and there are no keys. Recent expansions of European species to North America were missed (the establishment of *Hemithea aestivaria* (Hübner) in Canada was published in 1979); so range information outside Scandinavia and Finland is questionably thorough.

The English composition is awkward in only a few places—forgivable, considering the nationalities of the book's producers. Some typographical errors were found; and a number of words were broken in mid-syllable—irritating to a former English teacher! The print on coated paper is generally sharp, but there are numerous poorly impressed or broken characters which mar an otherwise lavishly produced book.

The expense of this book will unfortunately preclude its addition to the bookshelves of many amateur lepidopterists in North America and other parts of the lepidopterological world outside Europe. This is sad because it is a first-rate work, and is just one of many fine works on European moths that have recently come out. Those who specialize in Geometroidea should certainly find it a valuable investment.

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NOCTUELLES ET GÉOMÈTRES D'EUROPE. DEUXIÈME PARTIE. GÉOMÈTRES. Volume IV—1919–1920. Jules Culot. Reprint edition, 1987. Apollo Books, Svendborg, Denmark. Order from: Apollo Books, Lundbyvej 36, DK-5700 Svendborg, Denmark. Vols. III–IV, DKK 1380.00; Vols. I–IV, DKK 2550.00.

This is the fourth and last volume of the set, with 167 pp. and color plates 38–70 (Figs. 772–1403). It covers part of Larentiinae (beginning with *Eupithecia*) and Ennominae, although neither of these subfamily terms are used, much less defined. Having worked with *Eupithecia* of North America and Chile, I found the 45 pages and 140 figures devoted to this group particularly frustrating, as there are no descriptions or figures of genitalia; to me, a study of these structures is almost a necessity to correctly name many of the species. The same can be said about the species grouped together in *Boarmia*; in this case a number of different generic names are in use today.

Having reviewed Vol. III (J. Lepid. Soc. 41:239), I need not repeat comments made there, except to add that the text is in French in the entire set. This volume can be useful to determine some of the more obvious and distinct species, but the scientific names date from 1901. Much more up-to-date works are available and, to me, they could very well prove more useful than the volumes of this set.

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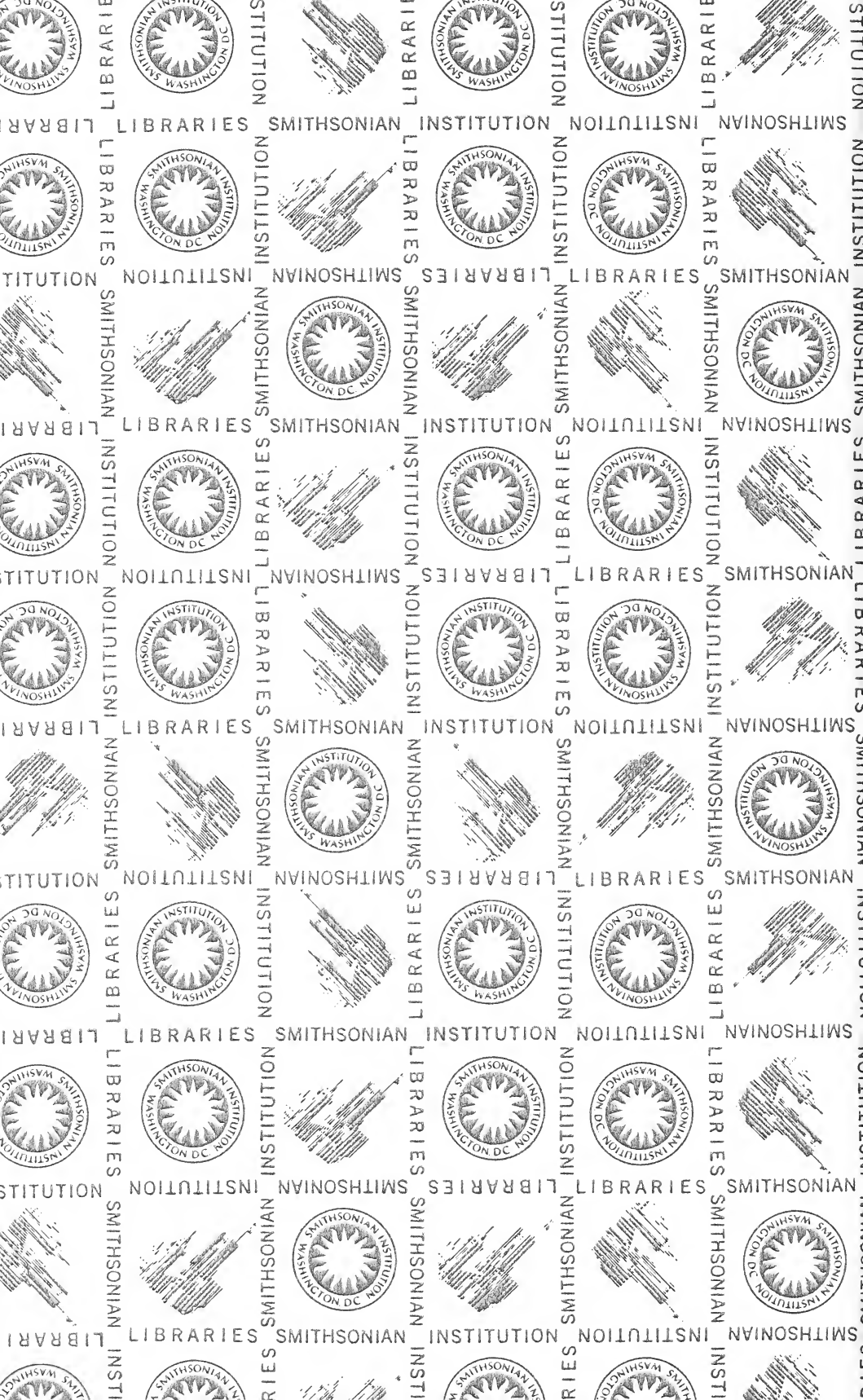
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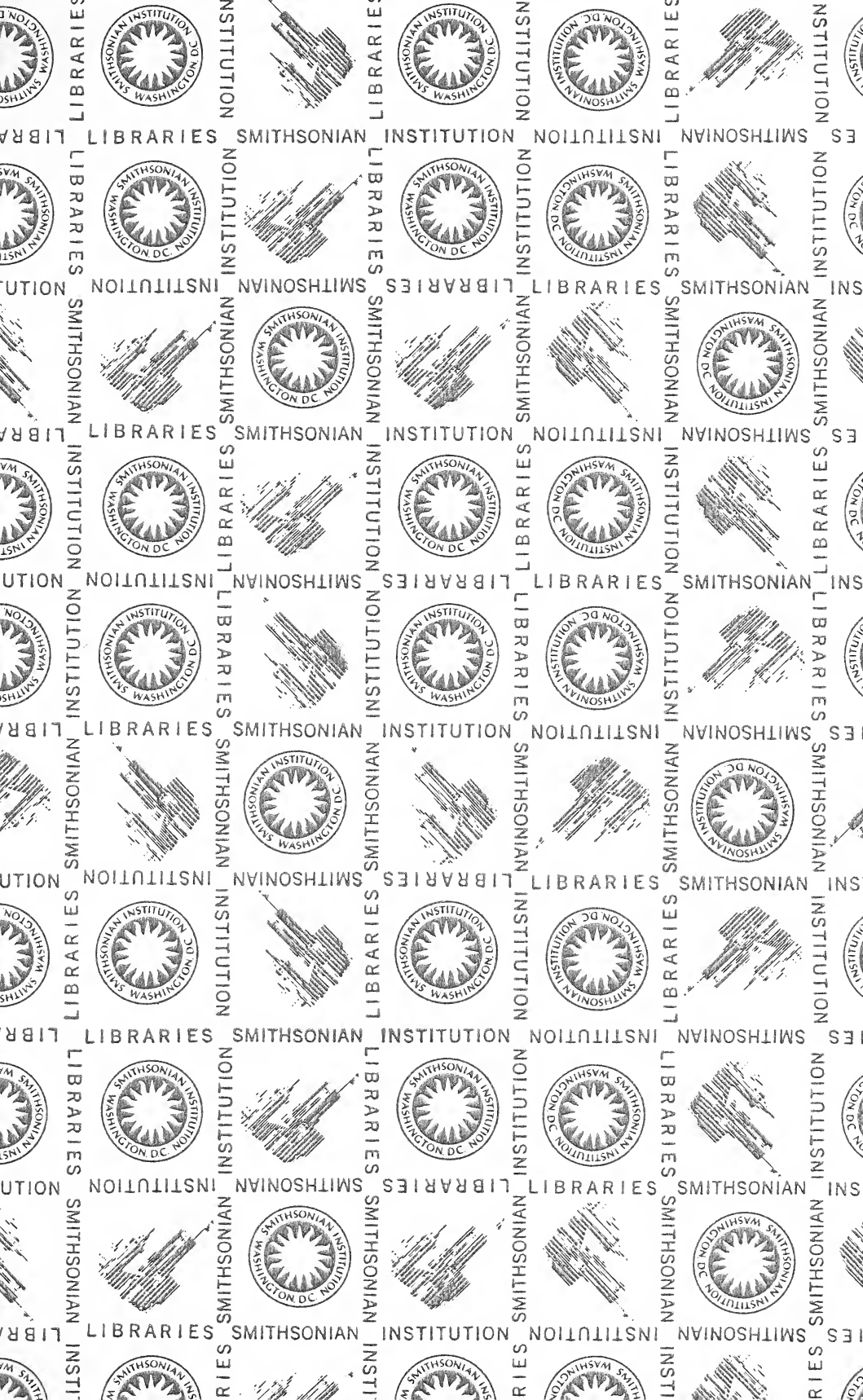
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